Linking Movement Ecology with the Management of Mobile Species

Managing Moose in Sweden

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Cover: The first moose I saw fitted with a GPS collar. Affectionately, she is known as Molly, but officially she is moose number 13_076. The map displays her movements from March'13 to March'16. She migrated ~110km every year, with a high overlap of migratory paths and summer and winter home ranges. She began her spring migration in late April (± 5 days) and she arrived at the summer range in early June (± 3 days). Autumn migration started in early November (± 21 days) and she arrived at the winter range in mid-December (± 25 days).

(photo: Andrew M. Allen)

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Abstract

A central goal in conserving, or managing, biodiversity is to identify the spatial scale of management. Traditional approaches like protected areas aim to delineate boundaries, within which species are managed. These boundaries are set using, among others, species richness targets and political borders, but often fail to consider species movements. Subsequently, a number of challenges may arise once individuals leave demarcated areas, such as poaching or encroachment on human-dominated areas. An ongoing dilemma is that many species cannot be managed within a single area because their movements are too large, migratory birds are a classic example. These challenges point to the requirement for an improved understanding of species' movements to not only delineate management areas, but also to identify alternative management actions that increase the scale and flexibility of management.

My dissertation identifies how movement ecology may guide wildlife management. I first outline a conceptual framework that provides guidance for linking movement ecology with conservation and wildlife management. The framework is then applied through a sequence of five studies that a) provide guidance on a method that classifies and quantifies movements, b) improves our understanding of how to scale up individual movements to population patterns, c) links the movement of individuals to their reproductive performance, d) estimates population size from age-specific harvest data and e) evaluates hunting of moose in Sweden using the ecosystem exploitation hypothesis. These studies were developed using the moose (*Alces alces*) in Sweden, an example of a species with diverse movement patterns that is typically managed in demarcated areas like moose management areas (e.g. Sweden) or wildlife management units (e.g. Canada). In a global context, the results of my dissertation illustrate how movement ecology may guide the management of mobile species, and nationally it complements the recently adopted moose management system in Sweden. Following my research, I encourage conservationists and managers to explore new ways of strengthening the link between movement ecology and management of mobile species.

Keywords: wildlife management, movement ecology, conservation, partial migration, protected areas, scale

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Dedication

To the moose of Sweden (and some in Norway too)

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Allen, A.M. & Singh, N.J. (2016). Linking movement ecology with wildlife management and conservation. *Frontiers in Ecology and Evolution* 3, art155

II Singh, N.J.*, Allen, A.M.* & Ericsson, G.E. (2016). Quantifying migration behaviour using net squared displacement approach: clarifications and caveats. *PLoS ONE* 11(3), e0149594
*Shared first authorship

III Allen, A.M., Månsson, J, Sand, H., Malmsten, J., Ericsson, G.E. & Singh, N.J. (2016). Scaling up movements: from individual space use to population patterns. *Ecosphere* 7(10): e01524

IV Allen, A.M., Dorey, A., Malmsten, J., Edenius, L., Ericsson, G.E. & Singh, N.J. (*submitted*) Habitat performance relationships of a large mammal on a predator-free island dominated by humans.

V Allen, A.M., Leonardsson, K., Singh, N.J. (s*ubmitted*) A simplified cohort analysis for estimating population size of managed large herbivores

VI Allen, A.M., Hobi, M.L, Radeloff, V.C., Leonardsson, K., Ericsson, G.E & Singh, N.J. (*manuscript*) Managing herbivore populations in the framework of exploitation ecosystems.

Papers I - III are reproduced with the permission of the publishers.

The contribution of Andrew M. Allen (AA) to the papers included in this thesis was as follows:

I AA formulated part of the idea and wrote the majority of the manuscript

II AA formulated part of the idea, performed the majority of the analyses and contributed equally to writing the manuscript

III AA formulated part of the idea, performed all the analyses and wrote the majority of the manuscript

IV AA formulated part of the idea, performed the majority of the analyses and wrote the majority of the manuscript

V AA formulated part of the idea, contributed to part of the analyses and wrote the majority of the manuscript

VI AA formulated part of the idea, performed the majority of the analyses and wrote the majority of the manuscript

Abbreviations

AIC	Akaike Information Criterion
BRB	Biased-random Bridge
CC	Concordance Criterion
DHI	Dynamic Habitat Index
EEH	Exploitation Ecosystems Hypothesis
GLM	Generalised Linear Model
GLMM	Generalised Linear Mixed-effect Model
GPS	Global Positioning System
IBPM	Individual-Based Population Model
LME	Linear Mixed-Effect model
MMA	Moose Management Area
NDVI	Normalised Difference Vegetation Index
NSD	Net-squared Displacement
PA	Protected Area
RMSE	Root Mean-Squared Error
RSF	Resource Selection Function
UD	Utilisation Distribution
UDOI	Utilisation Distribution Overlap Index
VHF	Very High Frequency
VIF	Variance Inflation Factor

1 Introduction

1.1 What is wildlife management and conservation

Wildlife management has been defined as the "management of wildlife populations in the context of the ecosystem" (Fryxell et al. 2014). The authors elaborate that several scholars may feel that this definition is too narrow, for instance people are excluded from this definition. A somewhat opposing view of conservation is outlined by Kareiva and Marvier (2012), whereby people are inextricably linked to ecosystems and the authors further advocate that conservation should occur for people and not from people. Human's presence in the landscape was recognised by Aldo Leopold, and he called for practices that integrated the habitat needs of wildlife with that of forestry, farming and other land uses (Leopold 1933). Nonetheless, Fryxell et al. (2014) stress that management activities are centred on manipulating or protecting a wildlife population to achieve a goal, and that the most important task is to choose the right goal and to know enough about the animals and their habitat to achieve that goal. Here I would like to stress *knowing enough about the animals and their habitat*. Conservation is needed when a population or species becomes threatened with extinction due to for example poor management, over-exploitation, habitat loss/degradation or stochastic events. Conservation actions generally aim to restore, or prevent the further decline of a population, species or ecosystem.

The fields of management and conservation have grown considerably in recent decades and incorporate several aspects that aim to improve the management process. Given the multi-use of the landscape, which may have conflicting land-use goals, multi-criteria decision analyses aim to take account of these competing criteria to guide the decision making process (Belton and Stewart 2002). It may also be that managers decide to undertake a number of actions to

achieve a management goal, and here techniques have been developed to prioritise actions with the greatest likelihood of success (Wilson et al. 2009). Systematic conservation planning provides a structured framework that enhances the planning process to identify the conservation needs, goals and how actions should be implemented and maintained (Margules and Pressey 2000). Meanwhile adaptive management aims to gain knowledge through the management process, which can be iteratively implemented as knowledge of the system improves (Williams 2011). Despite these advances in management and conservation, a common challenge that is shared in all these approaches is to identify the scale at which management actions need to be implemented.

1.1.1 A question of scale

Management actions have been traditionally implemented within areas that have clearly demarcated boundaries. Some examples include protected areas (PAs), wildlife reserves or game management areas. These boundaries are often set using, among others, species richness targets or existing political and administrative borders. The movements of animals within these boundaries were often excluded from the planning process, partly because little was known about species' movements. Over time, research has shown that even the largest PAs fail to fully protect a species (e.g. Thirgood et al. 2004). Classic examples include the long distance migrations of birds (Martin et al. 2007) and the nomadic movements of pelagic species (Game et al. 2009), but even an individual's daily movements may result in it leaving demarcated management areas (Minor and Lookingbill 2010). Once animals move outside of demarcated areas they are often exposed to exploitation (Holdo et al. 2010) or considered pests (Woodroffe and Ginsburg 1998). In addition, most management areas occur in a landscape where multiple types of natural resource extraction occur (Sanderson et al. 2002), potentially resulting in habitat degradation in surrounding areas (Ewers and Rodrigues 2008) and isolation through fragmentation (Chape et al. 2005). The future effectiveness of PAs is also being questioned, for example, as a result of climate change PAs may not track the changing distributions of species (Araújo et al. 2011, Singh and Milner-Gulland 2011a).

In recognition of the challenges associated with managing animal movements within static boundaries, alternative approaches are being developed to manage wildlife outside of demarcated areas. Some examples include temporary closures in marine and freshwater ecosystems (Hunter et al. 2006, Game et al. 2009) and wildlife corridors that improve landscape connectivity (Schmiegelow 2008). However, there has been much debate about the

effectiveness of approaches like wildlife corridors (Beier and Noss 2008, Gilbert-Norton et al. 2010). One of the criticisms is that it is not known whether species use wildlife corridors, and that they may draw attention away from some of the broader issues like improving the amount of high quality habitats (Hodgson et al. 2009). Nevertheless, these examples do highlight the need for an improved understanding of species movements. In the case of temporary closures, managers need to know when and where a species will be, and for wildlife corridors, we need knowledge about the types of habitats that can serve as a corridor and how species are able to move in a fragmented landscape. Until recently, this knowledge simply was not available but recent growth in the field of movement ecology is providing the knowledge needed to improve the effectiveness of management actions.

1.2 Movement Ecology

Animal movement has been studied for millennia, and even Aristotle made observations about the phenomenon of migration. The term "movement ecology" has only been coined more recently though, in the early 2000s, when the aim of this emerging discipline was to derive testable hypotheses and to link empirical work with theoretical models (Holden 2006). Since then, the field has grown rapidly; Nathan et al. (2008) presented a unifying framework for studying animal movement, Holyoak et al. (2008) identified research gaps, and others made several linkages to other fields of research, such as biodiversity (Jeltsch et al. 2013) and physiology (Jachowski and Singh 2015). One reason for the late emergence of movement ecology as a discipline is that traditionally, animal movement has been extremely difficult to study (see for example Box 1). However, a number of recent advances in the field, both in terms of tracking individuals and relating those movement tracks to environmental data, has provided new opportunities for studying animal movement.

Box 1 – Chasing the Grey-cheeked Thrush (*Catharus minimus*)

Amazing discoveries were made during the pioneering studies of bird migration. The following was described in Zimmerman et al. (1998). In 1965, Richard Graber fitted a grey-cheeked thrush with a radio transmitter in Chicago, and followed the bird by plane as it began its migration. He managed to follow the bird for 8 hours on a non-stop flight, but where the bird flew up the middle of Lake Michigan, Graber followed from the edge of the lake. Graber managed to follow the bird for nearly 650 kilometres, with the bird averaging 80kph, before Graber ran low on fuel and had to land. The thrush however, continued migrating northwards, its eventual destination unknown. These early studies revealed how little we knew about animal movement, such as the mobility of species in the landscape, where they went, how they navigated and what was driving these movements?

Photo: Steven Kersting

1.2.1 Advances in the field

Very high-frequency (VHF) radio transmitters yielded a number of insights about animal movements. VHF telemetry typically involved attaching a small electronic tag to a focal animal, which could then be tracked using a receiver and antennae from foot, vehicle or plane. The user had to be within a few kilometres to detect the tag, but as illustrated in the thrush example in Box 1, VHF was less suitable for tracking long distance movements due to the challenge of finding the tagged individual again. The onset of global positioning systems (GPS) has revolutionised animal tracking studies (Cagnacci et al. 2010, Kays et al. 2015). GPS triangulates an animal's location using satellites in space. Initial accuracy in the 1990s was intentionally restricted to 100m by the military (Moen et al. 1997). However, these restrictions were removed in 2000 and resulted in GPS accuracy improving to ~30m, and ongoing advancements mean that accuracy is often to within a few metres today (Tomkiewicz et al. 2010). A major advantage of GPS is that the animal's location can be collected with a high temporal resolution and accuracy, for example, locations have been collected at time intervals of seconds to map how soaring birds use thermals (Harel et al. 2016). The species that could initially carry GPS units were limited though, with the first GPS units weighing nearly 1kg (Tomkiewicz et al. 2010), and especially

considering the recommendations that a GPS unit should not exceed 5% of the animals body mass, or 3% for flying animals (Kenward 2000). However, again technology has moved forward and currently GPS trackers may weigh as little as 1.1g and can be used to accurately track the migrations of small songbirds (Hallworth and Marra 2015). Aside from GPS, a number of other advances have been made for tracking animal movements like stable isotopes (Rubenstein and Hobson 2004), light-level geolocators (Stutchbury et al. 2009), acoustic telemetry (Hussey et al. 2015) along with many more (Pimm et al. 2015, López-López 2016).

1.2.2 Applications

The advances in tracking animal movement has provided two key benefits, and the first is that it allows us to track species that were previously impossible to study (Hebblewhite and Haydon 2010). Some examples include tracking the trans-Atlantic journey of a great white shark (*Carcharodon carcharias*) that swam over 53,000km in two years[1] (more than double the distance that an average Swede would drive during the same timeframe[2]), or bar-tailed godwits (*Limosa lapponica*) migrating more than 11,000km in a non-stop journey lasting 8 days (Battley et al. 2012). The second benefit of recent advances in animal tracking is that they improve our understanding of species' ecology, such as space use patterns, home ranges and how biotic and abiotic factors influence movement (Cagnacci et al. 2010). This knowledge enables researchers to link an individual's behaviour and its fitness, and subsequently how this may influence population dynamics (Morales et al. 2010).

However, there are a number of challenges and concerns about the rapid growth of research in movement ecology. Many projects have only documented grand migration journeys without considering their ecological meaning. The growth of GPS technology has also meant that researchers have become disconnected from the field since the locations of animals are transmitted directly to their computer in the office, and researchers thus lose an understanding of the environment that the animal lives in (Hebblewhite and Haydon 2010). I have personally experienced this, and for example, I didn't truly appreciate how many moose (*Alces alces*) aggregated together during winter until I saw it with my own eyes in the field. Another problem with GPS technology is that it is expensive, meaning that researchers often only track a few individuals in space and time (Hebblewhite and Haydon 2010). The large intraspecific variation in movement patterns means that it becomes difficult to

[1] Based on data for a shark named Lydia, www.ocearch.org
[2] Based on driving statistics from www.trafa.se

infer population-level patterns, which is especially a challenge for management since management decisions are often based on a population mean. For example, movement data collected from a few individuals may be used to parameterise a landscape resistance model that describes an entire population (Spear et al. 2010). In addition, researchers should investigate how VHF or GPS tracking devices may affect the animal carrying it. Capturing the individual to fit the tracker may cause stress or injury, and it may experience additional negative effects from carrying the tracker, which may also affect the behaviour of the individual (Bridger and Booth 2003, Cattet et al. 2008). Despite these challenges, the recent advances in movement ecology have had a number of revelations for the management and conservation of wildlife populations.

1.3 Movement Ecology and Wildlife Management

The discoveries in movement ecology have created a paradigm shift when thinking about conservation and management. How can we conserve a species like the great white shark that moves more than 25,000km a year in an area that covers nearly half the North Atlantic? Key concepts like migratory connectivity have emerged (Webster et al. 2002), where it became evident that management actions need to include both the winter and summer ranges of migratory individuals and also the stopover sites along the migratory route (Martin et al. 2007). Landscape connectivity is another key concept in which movement is a vital component for providing ecosystem services like pollination (Kremen et al. 2007), or maintaining processes like dispersal and subsequent genetic diversity (Baguette and Van Dyck 2007). Here I return to section 1.1.1, a question of scale, and ask how can we manage species at the correct scale? Managed areas like PAs have a vital role in conserving biodiversity (Naughton-Treves et al. 2005), but alone they cannot achieve the scale of management necessary. Species movements are either too large or there are too many conflicting land-uses like housing, farming and forestry for PAs alone to be effective (Sanderson et al. 2002, Thirgood et al. 2004). This is where movement ecology can provide the knowledge needed to identify novel management actions that can improve the scale of management.

How movement ecology can benefit wildlife management has generally received less attention, not only in scientific literature, but also among peers. During my PhD I attended two conferences specifically in the field of

movement ecology[3] and another conference that was in the general field of conservation[4]. Few presentations in the movement ecology conferences discussed the management implications of their work, and in contrast, few presentations at the conservation conference included examples of how movement ecology was guiding conservation. To bridge these two fields, my dissertation work has focused on strengthening the link between movement ecology and wildlife management and conservation, both in the scientific literature and through presentations at the above mentioned conferences along with a number of national and international meetings. The concept can be applied very broadly, but in this dissertation, I specifically explore the moose management system in Sweden, and how an improved understanding of the movement ecology of moose may guide the spatial scale of management.

1.4 Managing Moose in Sweden

1.4.1 The Stakeholders

The moose is the largest deer species in Europe, and in Sweden it is affectionately known as the King of the Forest (skogens konung). The management of moose has implications for a number of stakeholders. The moose is an iconic species, it holds an aesthetic value for the general public and draws tourists to Sweden, especially since Sweden has the largest population of moose in Europe. The moose may also be seen negatively by the general public due to collisions with vehicles. For example, 4,914 vehicle collisions with moose were reported in 2015[5], which not only have monetary consequences for vehicle damage, but more importantly, a serious risk for personal injury or death of the people involved as well as the moose (Seiler 2005).

The moose has an important cultural value in society, and there is a long standing tradition of hunting. Hunting moose is not only a cultural experience, but is also seen by many as a form of recreation. Furthermore, moose meat can be considered as a provisioning ecosystem service (MA 2005), which is one of the main reasons for hunting in Sweden (Ljung et al. 2012). Therefore, a common goal for hunters is to have a large population of moose. However, another important stakeholder is the forest industry. Managed forests cover more than half of Sweden and the forest industry is one of Sweden's largest

[3] Movement Ecology & Dipsersal, Aberdeen, November 2013 and Animal Movement and the Environment, Raleigh, May 2014

[4] North American Congress for Conservation Biology, Madison, July 2016

[5] 2015 statistics from www.viltolyckor.se

industries. Although managed forests provide an ideal environment for moose (Edenius et al. 2002), moose come into conflict with the forest industry due to the damage they inflict. Moose cause browsing damage, particularly to young Scots pine (*Pices sylvestris*) during winter (Edenius et al. 2002), which stunts the tree's growth or even kills the tree, and ultimately reduces the economic value of the wood. In contrast to hunters, the forest industry aims to keep the moose population low to reduce browsing damage. The government, together with researchers and other stakeholders, needs to manage the population in a way that balances these conflicting goals.

1.4.2 Moose Management

In Sweden, the moose is managed through an adaptive co-management system that was adopted in 2012, details of which have been outlined by the Swedish Environmental Protection Agency[6]. The aim of the moose management system is to maintain a high quality moose population that is in balance with grazing resources and takes into account the public interests. A new spatial unit of management was introduced, called a moose management area (MMA), or älgförvaltningsområde (ÄFO) in Swedish. Each MMA is led by a moose management group, consisting of three landowners and three hunters as representatives who are jointly responsible for drawing up the moose management plan for the MMA. The guidelines state that the MMA should encapsulate at least 80% of a distinct population, and the scale of management should consider the movements of moose whilst roads and rivers should form the spatial boundaries of areas. The number of MMAs in Sweden is currently 149 and the guidelines state that the size should be at least 500km^2, although this may vary by region. The MMAs follow a general trend of increasing size from the south to the north of Sweden (Figure 1). The north-western most MMAs are the largest and the shape of the MMA aims to capture the directional movements of moose in this region. However, the movements of moose create a number of challenges for wildlife management, which is why movement is specifically incorporated in the design of the MMAs.

[6] http://www.naturvardsverket.se

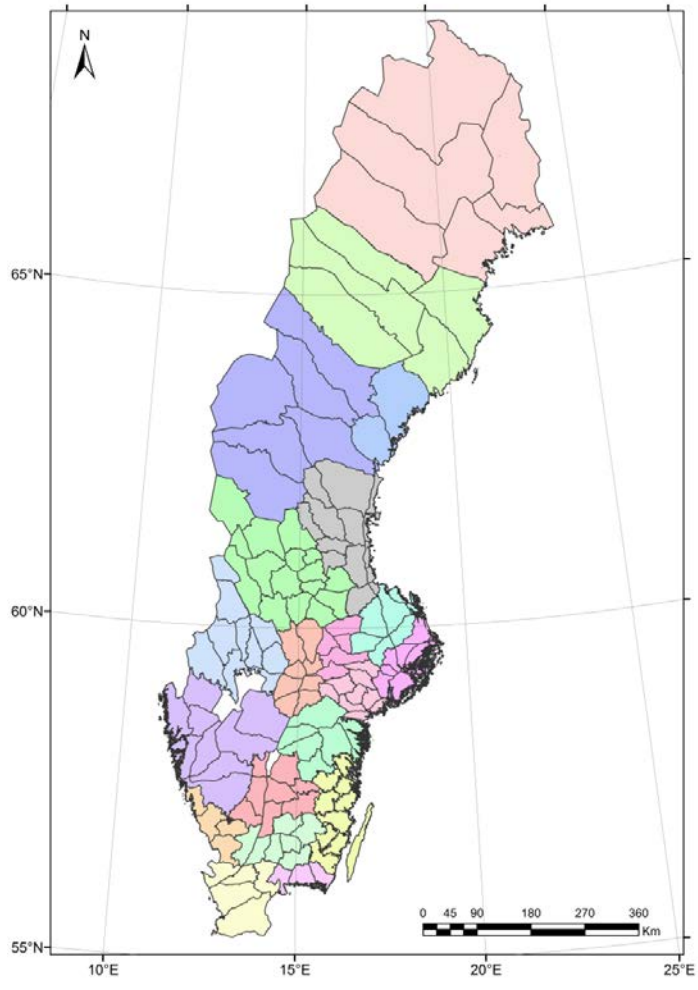


Figure 1 *- Map of the moose management areas (MMAs, n = 149) in Sweden. All MMA boundaries are demarcated by the black lines whilst the colours indicate the county administrative boards (Läns).*

1.4.3 Movement Ecology of Moose

Moose exhibit a complex array of movements across its distributional range. In Sweden alone, moose exhibit migratory, nomadic, sedentary and dispersal movements (Ball et al. 2001, Singh et al. 2012). Migration distances of over 200km have been recorded in Sweden, but at the same time migrations may be as small as 5km (Ball et al. 2001, Singh et al. 2012). Migratory movements have also been reported in a number of other countries such as Norway (Andersen 1991), Finland (Nikula et al. 2004), Canada (Hauge et al. 1981) and

USA (Phillips et al. 1973). The majority of migrations tend to be over shorter spatial scales that include migrations to either coastal areas or across altitudinal gradients, but some extreme migration distances have been reported in for example Alaska (see Berger 2004).

The Swedish moose population can be described as partially migratory, i.e. a proportion of the population migrates whilst others remain in the same area year round. Partial migration has important considerations for the ecology and evolution of a species, for example, migration may influence fitness and life history traits, and migrants and residents may ultimately speciate due to a lack of overlapping breeding ranges (Cagnacci et al. 2011, Chapman et al. 2011). Partial migration also raises a number of challenges for wildlife managers. In birds, sedentary populations may have higher extinction risks than migratory populations in the face of climate change, however, the types of threats these populations face may vary (Sekercioglu 2010). In contrast, several studies have shown that migratory populations of ungulates face a larger number of threats and have observed a general increase in the proportion of resident tactics in a population (Wilcove and Wikelski 2008, Hebblewhite and Merrill 2009, 2011). Partial migration also complicates the scale of management since it no longer becomes a question of managing a winter or summer range but instead management strategies need to adapt and incorporate both migratory and resident tactics. Partial migration would also influence monitoring efforts depending on when and where monitoring actions are taken and how the home ranges of sedentary and migratory populations overlap in summer or winter.

Moose not only have large variation in the types of movements (i.e. migratory, sedentary etc.) but also in their seasonal space use patterns. Studies have documented how space use may vary seasonally. For example, some studies found that individuals use larger areas during summer than winter, whilst other studies have found that individuals have larger home ranges during winter, or that there are no differences in seasonal home range size (Cederlund and Okarma 1988, Cederlund and Sand 1994, Hundertmark 2007). A number of factors may influence the size of the home range, including life history traits, forage availability, predator avoidance, snow depth and human disturbance (Olsson et al. 2011, van Beest et al. 2011, Bjørneraas et al. 2012, Basille et al. 2013). Understanding factors that influence space use is important for predicting home range size, a metric that is commonly used to define the scale of management (Schwartz 1999), understanding how space use may influence performance (i.e. survival and reproduction; McLoughlin et al. 2007, Gaillard et al. 2010) and for scaling up movements from individuals to populations.

Management actions are normally taken at the population scale and understanding what drives intraspecific variation among individuals is vital for deriving population-level patterns (Holdo and Roach 2013). A common challenge is that either too few individuals have been tracked or the geographic focus has been narrow meaning that the implications of a study are fairly localised.

1.5 Aims

The aim of my thesis is to improve the management of moose by incorporating knowledge of its movement ecology. A particular focus is to understand at which scale we should be managing moose given the complexity of movements and competing goals of stakeholders. Scale can incorporate both spatial and temporal components. Although moose are the target species in this dissertation, my aim has been to develop concepts that can be broadly applied beyond moose. The specific objectives of my thesis are to:

I. Develop a conceptual framework that can be used to improve the link between movement ecology and wildlife management
II. Improve the usability of methods that managers need to classify and quantify movements (e.g. timing, duration and distance)
III. Understand the causes of variation in space use patterns to scale up movements from individuals to populations
IV. Understand how space use patterns influence performance (reproduction)
V. Improve our ability to estimate population size and link monitoring capabilities with the scale of management
VI. Evaluate the role of hunters in the context of the exploitation ecosystem hypothesis

2 Methods

2.1 Conceptual Framework (Paper I)

As elucidated in the introduction, how movement ecology can benefit wildlife management has generally received limited interest. At the outset of this thesis, my aim was to improve this link and increase awareness about the benefit of linking movement ecology with wildlife management. I initially performed a literature review to understand what the challenges in managing mobile species are and how movement ecology can benefit the management of these mobile species. The literature review included identifying which management actions have been recently developed, what knowledge about movement is needed and how these management actions can complement existing approaches like PAs to achieve the scale of management necessary. I synthesised this knowledge into a conceptual framework, called the "Movement-Management Framework". The framework contained five steps that identify (1) the movement attributes of a species, (2) their impacts on ecosystems, (3) how this knowledge can be used to guide the scale and type of management, (4) the implementation, and (5) the evaluation of management actions (Figure 2). Paper I introduces the framework in detail, describing each of the steps along with a number of considerations (Figure 2).

We illustrated the framework using a case study of a highly mobile species with a complex array of movements, Atlantic salmon (*Salmo salar*). In my dissertation, I also apply the movement-management framework to moose. I include a summarising overview of managing moose in Sweden, following the structure of the movement-management framework and incorporate the results of previous studies along with my own findings in Papers II to VI. The sections that follow describe the design, development and implementation of Papers II to VI and finally links these back to the movement-management framework.

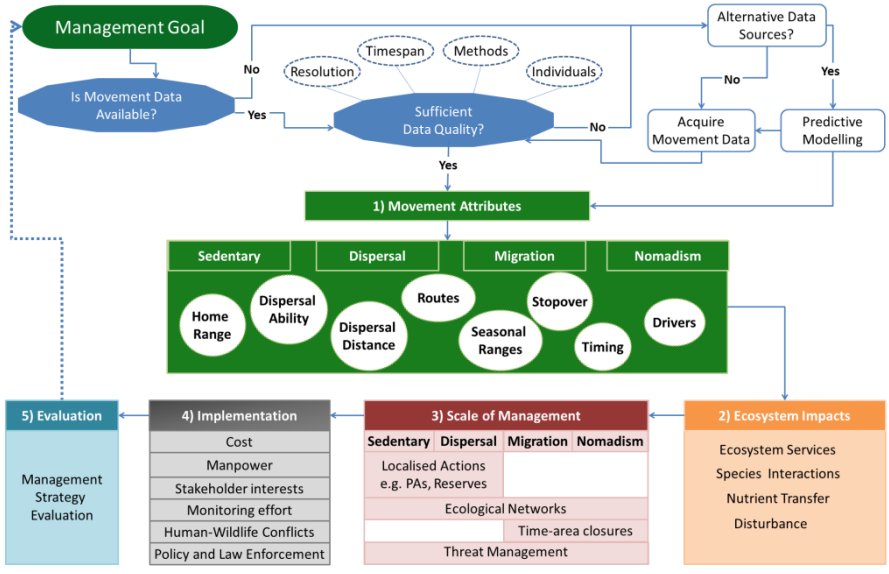


Figure 2 *- Movement-Management framework that provides a workflow for incorporating movement ecology into the decision-making processes. The framework contains five steps that identify (1) the movement attributes of a species, (2) their impacts on ecosystems, (3) how this knowledge can be used to guide the scale and type of management, (4) the implementation, and (5) the evaluation of management actions. Before implementing these steps, managers need to consider whether movement data is available, of sufficient quality and whether alternative sources of data are available. Our framework can be flexible and adapted to manager's needs. For example, McGowan and Possingham (2016) include an additional step to consider how management may change with improved knowledge of movement and the value of information.*

2.2 Study area (Papers II – VI)

In general, the studies conducted in my dissertation have included the entirety of Sweden and even parts of northern Norway (Paper III). Papers II and III incorporate movement data for ten moose populations that span a latitudinal gradient of nearly 1,500 km (Figure 3). Paper IV focused on the population we have labelled S4 (Figure 3), which is an island population of moose on Öland. Papers V and VI on the other hand incorporate data from all MMAs (Figure 1) and thus cover the whole of Sweden, except for Gotland where no moose occur. The structure of MMAs has changed since the new moose management system was adopted in 2012. Originally there were 147 MMAs, but some of these have been divided to create the 149 occurring today. I collated the data

for the additional two MMAs to maintain the original structure of 147 MMAs, and thus data were comparable from the adoption of the new moose management system (2012) through to today (2016).

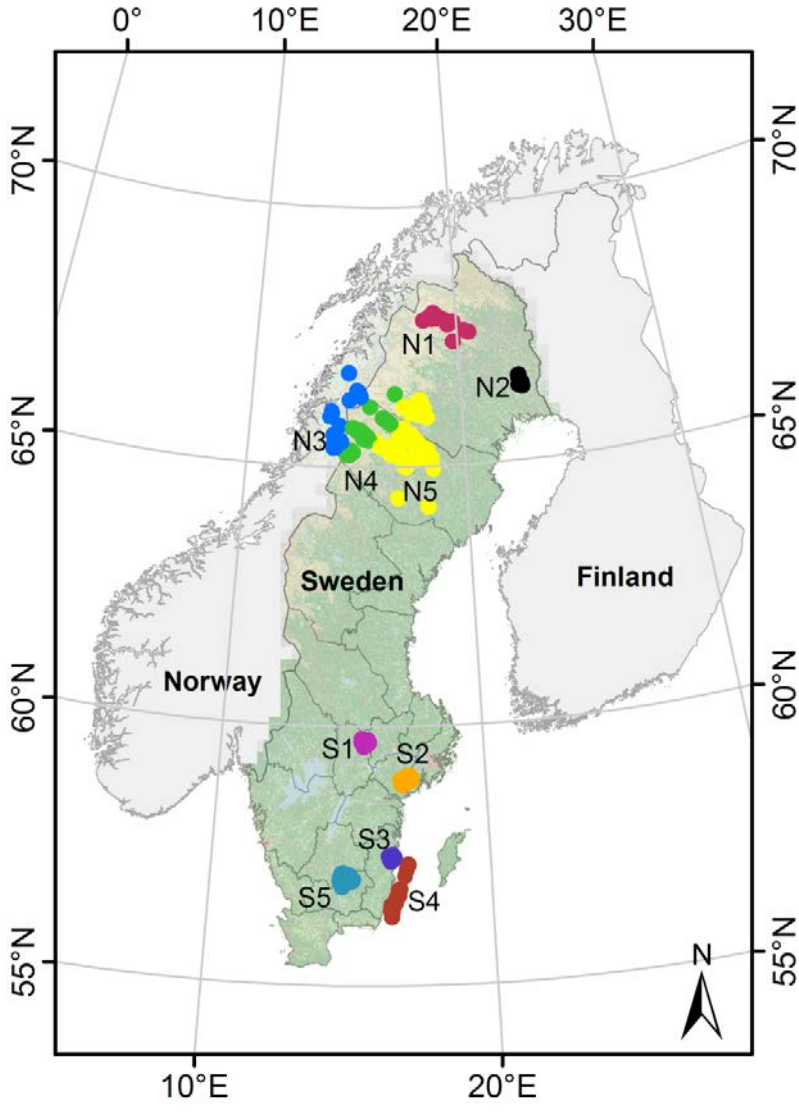


Figure 3 *- Study area map showing the ten study areas, five in the north (N1, N2, N3, N4, N5) and five in the south (S1, S2, S3, S4, S5). The coloured locations indicate the average winter location for each moose and study area. The coloured map of Sweden indicates the approximate habitat types in Sweden showing forest habitats in green, open habitats in yellow, urban areas in grey and freshwater as blue.*

Sweden is dominated by forestry through most of the country although the proportion of broadleaf and coniferous forest may vary (Figure 4). The south of Sweden and coastal parts of northern Sweden are dominated by coniferous forest (e.g. N2 and S5; Figure 3 and 4). In contrast, the high elevational regions in the north-west of Sweden have higher proportions of broadleaf forest (e.g. N3 – N5; Figure 3 and 4). Coniferous forests are generally dominated by Scots pine and Norway spruce (*Picea abies*) whilst broadleaf forest are dominated by birch species (*Betula spp.*) with rowan (*Sorbus aucuparia*), aspen (*Populus tremula*) and willow species (*Salix spp.*) interspersed throughout. The large latitudinal gradient across the study area means that there are also a number of environmental gradients. Vegetative productivity tends to be higher in the south of Sweden, which also has longer growing seasons, lower snow depths and shorter periods of snow (Figure 4). The human presence in the landscape also follows a gradient, as indexed by the proportion of arable land and road density, with greater human presence in the south than in the north (Figure 4).

Study area S4 (Paper IV) stands out from the other study areas, as seen in the proportion of arable land (56%) and forested habitats (21%; Figure 4). Öland (S4) is located in south-east Sweden (Figure 3) and is Sweden's second largest island (~1,342km^2 and 137km in length). Öland has been intensively used for farming and livestock grazing over the last few centuries. Much of the wooded areas today originate from encroachment after cessation of grazing and abandonment of marginal farmland. The forests in the north have been heavily utilised by the timber industry for more than a century. Öland has a large proportion of alvar grasslands (19%), which are found over dry, shallow, nutrient poor grazed soil on top of limestone bedrock. A large alvar, the Stora Alvaret, is located in the southern part of Öland (~255km2). Paper IV divided Öland into two study areas, north and south, with the extent of the Stora Alvaret separating these two areas.

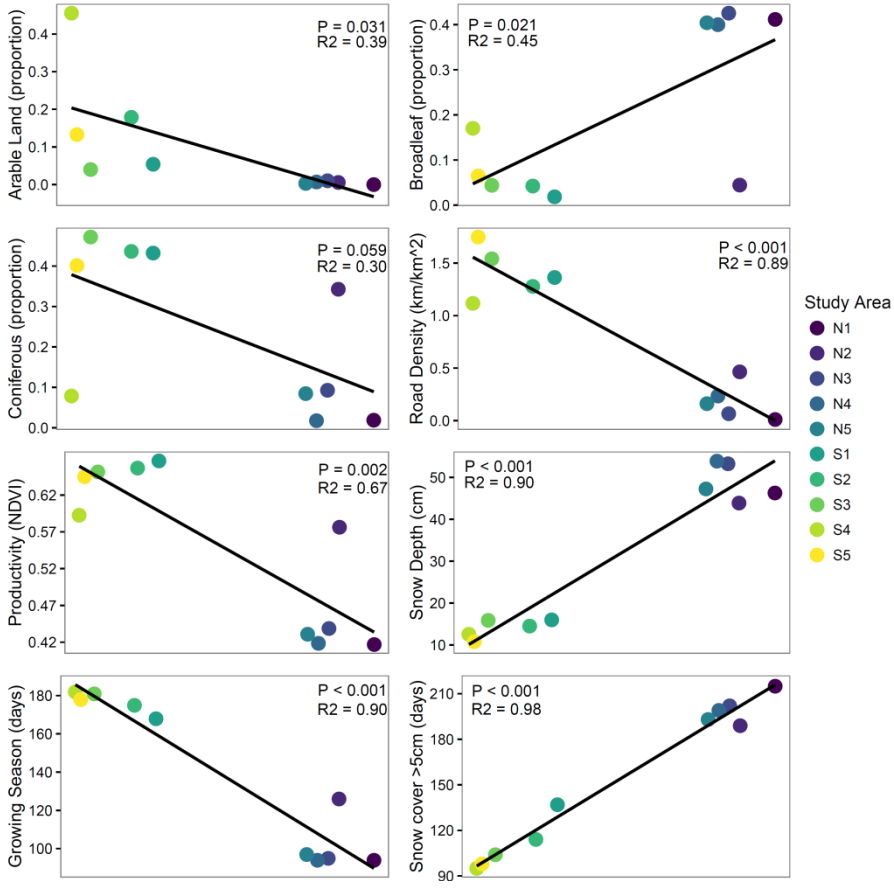


Figure 4 *- Landscape characteristics for the ten study areas consisting of five areas in the north (N1 – N5) and five areas in the south (S1 – S5) of Sweden. Landscape characteristics are shown as a series of regressions to illustrate the latitudinal gradient (x-axis) in a number of variables indicating human presence (e.g. Arable Land, Road Density), forest types (e.g. Coniferous, Broadleaf), productivity measured using the normalised difference vegetation index (NDVI) and the length of growing season, and period of snow cover that is greater than 5cm. The strength of the correlations are indicated by p-values and adjusted r-squared, and were estimated using a linear regression model.*

2.3 Movement Data (Papers II – IV)

Moose movement data has been collected using GPS collars across the ten study areas described in Figure 3. Animals were sedated and equipped with a GPS neck collar (Vectronic Aerospace GmbH, Berlin, Germany) during winter

and the data were managed through wireless remote animal monitoring (WRAM; Dettki et al. 2014). The sample size has varied depending on the study requirements but include 319 individuals in Paper II, 307 individuals in Paper III and 17 individuals in Paper IV. The time period of tracking ranges from 01 March 2004 to 01 July 2015. The data were screened to remove likely GPS errors, which can be detected by GPS locations being too far apart or uncharacteristic changes in the direction of movement (Bjørneraas et al. 2010). The GPS collars were programmed to record a GPS location every 30 minutes (48 locations per day), however these were also resampled to one location per day (Paper II & III) for applying the NSD method, four locations per day for estimating the home range (Paper III) or eight locations per day for estimating the home range and to identify habitat selection (Paper IV). In all papers, individuals that were tracked for less than one year were excluded whereas individuals that were tracked across multiple years had their trajectories split into years. The total number of single year trajectories available for each study were 489 (Paper II), 544 (Paper III) and 45 (Paper IV).

The size of the movement dataset provided a number of opportunities for understanding the movement ecology of moose, but it was also daunting in terms of data management. The most recent dataset I handled (06 June 2016) contained 16,791,585 GPS positions, and even after filtering the data for Paper III, the number of GPS positions remained nearly 800,000. The size of the dataset has required careful consideration of how to manage such large datasets (Borer et al. 2009). The moose movement dataset used in this dissertation already covered a country-wide scale and included study area S1 through collaboration. There has also been a general call to merge datasets across different studies to expand the scale of research and achieve novel ecological insights (Hampton et al. 2013), which will further exacerbate these data management challenges. An example of such a collaborative network is the EURODEER project for roe deer (*Capreolus capreolus*; www.eurodeer.org), which has already produced a number of insights about roe deer ecology (e.g. Cagnacci et al. 2011, Morellet et al. 2013, Debeffe et al. 2014). Forming such a working group for moose in Northern Europe for example, would extend our ability to study the movement ecology of moose across environmental and climatic gradients.

2.3.1 Classifying Movements (Papers II – IV)

Moose exhibit movement types that include migratory, sedentary, nomadic and dispersing. Therefore, it is important to classify these movement types to not only understand how this may affect the scale of management, but also for

identifying when and where a species will be and to define periods that moose are in their summer or winter home range (e.g. Paper III). The size of the movement dataset means that visually categorising movements, an approach that is commonly used for smaller datasets (e.g. D'Eon and Serrouya 2005, Mysterud et al. 2011), becomes unviable. We used a recently developed, model-driven approach, for classifying movement that uses the net-squared displacement (NSD) of a movement path (Bunnefeld et al. 2011a, Börger and Fryxell 2012). The method measures the distance between every GPS position and the starting position, which is then squared (NSD). Bunnefeld et al. (2011) developed a number of models that describe the movements of migratory, sedentary, nomadic and dispersing individuals. These models are fitted to the NSD and the best fitting model describes the type of movement, which is determined by using either the akaike information criterion (AIC; Bunnefeld et al. 2011a) or the concordance criterion (Huang et al. 2009, Singh et al. 2012). A number of researchers have run into difficulties when using the method, either due to incorrect classification of movements or difficulties in obtaining model convergence (e.g. Mysterud et al. 2011, Bischof et al. 2012, Cagnacci et al. 2016). Given my own previous experience in applying the model in a novel manner to the daily movements of red deer (*Cervus elaphus*; Allen et al. 2014), and the experience of our group (Singh et al. 2012), we provided methodological guidance for using the NSD method (Paper II).

Paper II addresses three key questions that we have observed about using the method from previously published literature, discussions among peers and our own observations from using the NSD method. These questions were:

a) What is the effect of the extent of movement of a species on it being classified as migratory?
b) What is the effect of the selected starting date, and starting location, of the animal on the movement mode classification and parameters?
c) What is the effect of the data resolution on the model fit and resulting interpretations?

We addressed question (a) using the full movement dataset (n = 319 individuals), which included the four movement types and annual displacements that ranged from just a few hundred metres to more than 200 km. To address question (b) and (c), we filtered the movement dataset to contain just 41 migratory individuals that were tracked over the same timeframe (01 March 2008 to 28 February 2010). We then re-ran the NSD

models to determine how different starting dates, starting locations[7] (i.e. single random location, mean location in the first week, mean location in the first month) and data resolutions (one location per day, 48 locations per day, mean location per day) affected model performance.

Paper II provided a number of recommendations and considerations about using the NSD approach to classify movement modes. We applied these recommendations in Paper III and IV when classifying movement types of individuals. The NSD approach was also used to obtain the individual-level distance, timing and duration of migratory movements in Paper III and IV. Obtaining individual-level timing of migratory movements allowed us to identify individual-specific winter and summer home ranges, an approach that was much appreciated by the reviewers. All models were fit using the nlme package (Pinheiro et al. 2006) within the R environment for statistical computing (R Development Core Team 2012).

2.3.2 Home Range Estimation (Papers III & IV)

The home range has been described as the interplay between the environment and an animal's understanding of that environment (Powell and Mitchell 2012). The home range provides a measure of an individual's space use patterns and changes in home range size may be related to spatial, temporal and individual-level processes (Börger et al. 2006, Putman and Flueck 2011). Therefore, the home range provides a measure for understanding how changes in the environment, or the life history traits of an individual, lead to variation in space use patterns among individuals. Understanding the causes of variation in space use patterns of individuals would enable predictions of the scales of movement in a population, understand how future changes like habitat loss and degradation may influence space use patterns (Andren 1994, Wiegand et al. 1999, Fahrig 2007), and determine how the space use patterns of an individual may influence reproduction and survival, otherwise known as habitat-performance relationships (McLoughlin et al. 2007, Gaillard et al. 2010). Paper III investigated causes of intraspecific variation in home range size, but whereas most studies focus on a single geographical area, we were able to investigate variation among ten different populations (Figure 3), and among individuals within each of these ten populations. Paper IV focused on one study area, S4 (Figure 3), to understand how a female's space use patterns influenced reproduction and calf survival.

[7] Naturally changing the starting date will have an effect on an animal's location, and this aspect is incorporated in our analysis of starting dates. By starting location, we only refer to using a single random starting location or a mean location across a specified time period.

We calculated home ranges at an annual scale and a seasonal scale (summer and winter). The timings of migration were used to define the temporal scale of summer and winter home ranges for migratory individuals. This approach could not be used for sedentary individuals though. We investigated whether it would be possible to use the movement rates of sedentary individuals instead, as suggested by Vander Wal and Rodgers (2009) and van Beest et al. (2013), but without success (details in Paper III). Instead, we used factors that have previously been identified to be important for moose. We used the start and end of the growing season to define the summer home range, and the arrival and melt of snow to define the winter home range. These values were calculated for each population and year (see 2.4 Environmental Data) and thus all sedentary individuals would be exposed to similar conditions each season.

Home ranges were calculated using the biased-random bridge (BRB) approach (Benhamou 2011). The BRB calculates an utilisation distribution (UD) and is thus a kernel method for estimating home ranges. The BRB explicitly considers the movement of the individual when estimating the kernel, and for example, the probability of use will be higher between two known locations, as opposed to alternative methods where the probability of use is random around each location (Horne et al. 2007, Benhamou and Cornélis 2010, Benhamou 2011). Home ranges were calculated using the package adhehabitatHR (Calenge 2006). The diffusion coefficient was estimated using the BRB.D function and the smoothing parameter, hmin, was calculated as the mean inter-location distance divided by two (Benhamou 2011). The home range was defined by the 95% isopleth to exclude outlying and exploratory movements. I computed the home range size, which is the explanatory variable in Paper III, and also extracted the UD for each individual for later analyses. The UD was used to extract environmental data related to the home range, such as the proportion of certain habitats, the terrain, productivity and snow depths. Home range overlap was calculated in Paper IV and we used the kerneloverlapHR function to estimate the utilisation distribution overlap index (UDOI), a metric that has been shown to perform better when computing overlap of utilisation distributions (Fieberg and Kochanny 2005). Note that home range overlap was among seasons for the same individual (e.g. summer 2012 versus summer 2013), as opposed to the level of home range overlap among our different study individuals.

2.3.3 Habitat Selection (Paper IV)

To understand the non-random use of habitats within the home range, and how their use may influence individual performance, we analysed habitat selection using a resource selection function (RSF; Manly et al. 2007). We investigated third order habitat selection, which compares the habitats used to those available within the home range (Johnson 1980, Thomas and Taylor 1990). The used and available habitats were extracted from the Swedish Land Cover Data map (Hagner et al. 2005), which is described further in section 2.4 Environmental Data. Used habitats were measured at each GPS location (8 locations per day) and five random points were generated to measure habitat availability. The random points were measured within a 415m buffer of the GPS location, which captured 90% of distances travelled in a three hour period (Johnson et al. 2002, Boyce et al. 2003, Northrup et al. 2013). The RSF was estimated using binomial logistic regression and fitted using a generalised linear mixed-effect model (GLMM) to incorporate the mixed-effect design of the study (multiple observations per individual). We included a random slope and a random intercept to capture differential use of habitats and variation among individuals (Gillies et al. 2006, Hebblewhite and Merrill 2008).

2.4 Environmental Data (Papers III - VI)

The ability to map the environment in ever more detail has developed alongside the rapid growth in technologies for tracking animal movement (Turner et al. 2003, Pettorelli et al. 2014, Neumann et al. 2015, Kays et al. 2015). Databases for managing telemetry data, such as MoveBank (www.movebank.org) and ZoaTrack (www.zoatrack.org), now provide options to automatically link GPS locations to environmental data (Dodge et al. 2013, Dwyer et al. 2015). Obtaining, managing and creating environmental datasets has been an integral component of this dissertation. Identifying the environmental conditions has been a prerequisite for understanding the space use patterns of moose (Paper III and IV) and to relate environmental factors to harvest rate and population density (Paper VI). The preparation of the breadth of datasets used in this dissertation cannot be given justice here, and are mostly described in Appendix 2 of Paper III. However, Table 2 provides a summary of the environmental datasets used during my dissertation, how they were obtained or created, and the papers in which these datasets were used.

Table 1 – *Details of the environmental data included in this dissertation. The name of the environmental variable is given along with the date the data were delivered. The data are briefly described along with details of whether it was obtained, modified or created. The original source of the data are provided and the papers in which the datasets were used. The preparation of most datasets is described in Appendix S2 of Paper III except for the data not used in Paper III. The preparation of the other datasets is described in the relevant paper.*

Environmental variable	Description	Source	Papers
Land Cover data I 2003	Obtained and modified to age forests/apply new clear-cuts and summarised to 10 habitat classes instead of 60	Swedish Land Cover Data (www.lantmateriet.se)	III, IV
Land Cover data II 2000, 2006, 2012	Obtained and modified to contain 10 habitat classes instead of 35	Corine Land Cover Data (www.eea.europa.eu)	IV, VI
Normalised Difference Vegetation Index (NDVI) 2003 - 2016	Obtained and modified through quality control, smoothing and by setting a winter baseline.	MODIS – MOD13Q1 (www.lpdaac.usgs.gov)	III
Terrain (Elevation, Slope, Northness) 1999	Elevation data were obtained and used to create Slope and Northness rasters	www.lantmateriet.se	III
Snow depth 2003 - 2014	Weather station data were used to create daily rasters of snow depth (~4000 snow cover maps)	www.smhi.se	III, IV
Temperature 2003 - 2014	Same as snow depth	www.smhi.se	III, IV
Growing Season 2003 - 2014	Method of Karlsen et al. (2007) to calculate growing season from temperature data	www.smhi.se	III, IV
Dynamic Habitat Indices (DHI) 2003 - 2016	Obtained. Contains data on annual productivity, minimum productivity and seasonality	www.silvis.forest.wisc.edu	VI
Road Density 2013	Created from road map of Sweden	www.lantmateriet.se	III

2.5 Life History Data (Papers III – VI)

The life history traits of an individual may also be important for explaining variation in movement patterns. Space use patterns may stabilise as individuals age, gain experience and learn its environment (Dukas 1998, Saïd et al. 2009, van Moorter et al. 2009). The age of the individual may also influence reproductive performance through experience in raising young or senescence (Ericsson et al. 2001, Forchhammer et al. 2001). The sex of the individual may be important for explaining variation in space use patterns, either due to body

size requirements (e.g. Mysterud et al. 2001) or the differing drivers of movement for males and females (Testa et al. 2000, Neumann et al. 2009). We included both sex and age as explanatory variables in Paper III and in Paper IV we investigated how age may affect reproductive performance. Understanding the age of an individual was also important for estimating population size from harvest data as we illustrate in Paper V. In Paper III and IV, the age of an individual was estimated by the tooth wear, a method commonly used for ungulates (Ericsson and Wallin 2001, Rolandsen et al. 2008). We assume that hunters followed the same guidelines when ageing harvested individuals in Paper V.

Identifying the calving status of females was an important component of Paper IV. The presence/absence of a calf, or twins, was recorded by tracking females on three separate occasions during each year following standard operational procedures (see Ericsson et al. 2001). The three occasions were 1) during the calving season (May and June), 2) before the annual moose hunt (late September) and 3) during late winter (February/March). Females were checked on several occasions during the calving season to accurately record the calving date in the field. In addition, GPS data were checked every 12 hours to determine whether a female's movement rate had declined and become confined to a limited area, which may indicate that a female is about to calve (Testa et al. 2000). The calf (or calves) was usually found within three days of birth. If the calf was not observed during the follow-up checks, additional checks were made to ensure we did not record a false mortality event.

2.6 Harvest Data (Paper III – VI)

We obtained moose harvest data from www.algdata.se for the period 2012 to 2016. The harvest data included basic age and sex information (i.e. calf/adult and male/female) for all felled moose. The harvest data were used as an index of moose density in Paper III and we calculated moose biomass using data from PanTHERIA (Jones et al. 2009) to test for density-dependent effects on home range size in the ten study populations (Figure 3). We also used the harvest data to report population trends on Öland (Paper IV). The method developed in Paper V for estimating population size relied on age-specific harvest data. Finally, in Paper VI, we framed our approach for evaluating the role of hunters in the landscape around the Exploitation Ecosystem Hypothesis (EEH; Oksanen et al. 1981) and calculate the harvest rate (moose felled per 1000 ha).

We also included moose harvest data for the Norwegian population labelled N5 in Paper III (Figure 3), obtained from www.ssb.no. Papers III and IV also report harvest data for other ungulates, namely roe deer, red deer, fallow deer (*Dama dama*) and wild boar (*Sus scrofa*). Moose occur in a multi-species system with a number of other ungulates. Roe deer occur over most of Sweden, except for the far north and high elevation areas. Red deer and fallow deer occur over large parts of southern Sweden with some escaped populations in northern regions like south-east Västerbotten. Wild boar also occur over large parts of southern Sweden and their range is expanding (Massei et al. 2015), which may also be due to climate change (Vetter et al. 2015). Harvest data for other ungulates in Sweden was obtained from www.viltdata.se whilst Norwegian data (Paper III) was obtained from www.hjortviltregisterat.no. Harvest data of other ungulates was used to calculate a biomass value of other ungulates to account for inter-specific competition in Paper III. In Paper IV, we compare the harvest of roe deer between Öland and mainland Kalmar. The roe deer has a large diet overlap with moose (Mysterud 2000) and may compete with moose, particularly during winter. Hunters have reported a large increase in roe deer populations and for example the harvest rate of roe deer is much higher on Öland than in the rest of Kalmar.

2.7 Statistical Analyses

2.7.1 Paper III

Variation in home range size among populations, and within each population, was analysed using linear mixed-effect models (LMEs). The log of the UD95 was used as the response variable and the life history and environmental data described in sections 2.4 and 2.5 were included as explanatory variables. In addition, we included the variable "Time" to determine whether our method for determining seasonal home ranges was a cause for variation. We performed the analysis for two seasons, summer and winter. We used the package lme4 (Bates et al. 2014) in R to fit the models. We performed an explorative analysis to identify the best fixed-effect structure of the model. Models were ranked using AIC (Burnham and Anderson 1998), with a penalty for adding additional parameters (AICc). We calculated akaike weights for models with a delta AIC (ΔAIC) less than four and measured the amount of variation explained by the model using the r-squared statistic. Mixed-effect models include marginal R^2, the variation explained by fixed-effects only, and conditional R^2, the variation explained by both the fixed and random effects (Nakagawa and Schielzeth 2013).

Analysing variation among and within populations may create some confusion about study design. Analysing variation in home range size among populations combines all data across our ten populations to determine which environmental variables explain broad-scale variation in home range size. Therefore, the random-effects structure of the analysis is individual nested within study area (n = 10). It should be noted that only females were used in this analysis due to the low sample size of males in some populations. Analysing variation within populations meant fitting an LME to each study area, resulting in 20 sets of models results (i.e. 10 study areas for winter and summer). The random-effects structure included individual since some individuals were observed over multiple years. The analysis included both males and females, and included environmental variables that may explain fine-scale variation in home range size – i.e. among individuals in the same study area. We excluded variables with a high correlation coefficient from the analysis ($r > 0.7$), but also checked models for collinearity using variance inflation factors (VIFs; O'Brien 2007). Some study areas had low sample sizes (n < 30), therefore we constrained the analysis within populations to a maximum of three explanatory variables to avoid overfitting the model.

2.7.2 Paper IV

To understand habitat-performance relationships on Öland, we included two levels of analysis that were i) to investigate whether a female's space use pattern in the summer affected the number of calves born the following spring (i.e. fecundity), and ii) to investigate whether a female's space use pattern in the winter prior to calving, or in the summer after calving, influenced the survival of the calf. We used Poisson regression to investigate (i), where the response variable was the number of calves born (0, 1 or 2) and the explanatory variables were habitats generally preferred by moose and should thus result in higher body condition in the autumn, the time of reproduction (Testa and Adams 1998).

To investigate (ii), factors influencing calf survival, we considered two alternative hypotheses for which a number of candidate models were developed. The alternative hypotheses were that a) the use of habitats in the winter prior to calving would influence the female's body condition at parturition and thus affect calf survival (Parker et al. 2009, Mathisen et al. 2014), and b) the use of habitats in the summer after calving would influence the female's ability to meet the demands of lactation and thus affect calf survival (Gustine et al. 2006, Parker et al. 2009). We used binomial logistic regression to investigate these hypotheses and the response variable was

whether the calf survived (yes/no) to the autumn (but before the hunt), a metric normally considered to be the recruitment into the population. Some females were tracked over multiple years, therefore we determined whether the model should be fitted with a mixed-effect structure. The variance explained by the random effect was estimated to be zero given the data, suggesting that 1) the individual variance was very low, or 2) the data (i.e. low sample size) did not support estimating random variance among individuals, or a combination of both. Therefore, we fitted the logistical regression using a generalised linear model (GLM) using the R package lme4 (Bates et al. 2014). The explanatory variables were the proportion of time spent in each habitat, as recorded by the GPS location of the animal. The top three models for each alternative hypothesis are displayed along with a combined model that links the hypotheses together, and also includes the variables of age, twinning status, winter home range size and the daily movement rate during winter.

The fixed-effect structure of the model was determined using AICc and we used VIFs to check for co-linearity in the model. We reported the coefficient of determination, a measure of pseudo R^2, but since R^2 values for logistical regression are often less than one, we reported the adjusted R^2 which has been transformed to have a maximum of one (Nagelkerke 1991). We reported the akaike weights of the top three models (determined from all possible model sets with a $\Delta AIC < 4$) and estimated the relative variable importance (RVI; determined from all possible model sets). After determining the fixed-effect structure for the top three models in each alternative hypothesis, we used hierarchical partitioning to describe how important each variable was for explaining variation in calf survival (MacNally 1996). Hierarchical partitioning has been described as the best way for identifying the most important variable from a set of already identified top models (Murray and Conner 2009).

2.7.3 Paper V

The aim of Paper V was to develop a simplified method for estimating current population size from age-specific harvest data. Under the assumption of a stable population with a stable age structure, we used a simplified cohort analysis to estimate survival from harvest data, which can then be divided between natural mortality and harvest mortality. A likelihood function was used to determine harvest mortality. Given that we know the number of individuals that were harvested, the total population size can be estimated once harvest mortality is known. We validated our approach using empirical data and data from a simulated population.

An individual-based population model (IBPM) was parameterised to simulate a fairly stable population size over time. The simulated IBPM could be harvested, included natural mortality and recruitment was also applied in the spring. Each individual in the IBPM received a unique ID meaning it could be tracked through the model and thus the age of all individuals in the model were known. This meant that the age-specific harvest data extracted from the IBPM could be used in our simplified method, and the results of our method could be compared to the known population size in the IBPM to determine its accuracy and precision. The precision of the method may depend on the number of individuals harvested (i.e. sample size), and the IBPM could therefore be used to determine how sample size influenced model performance. In a real-life scenario, adjusting the sample size may be achieved by aggregating data over years or by aggregating data spatially across areas to achieve larger sample sizes. Determining the level at which the method begins to perform well may guide managers in determining the scale of management when the goal is to accurately estimate population size – a common goal for harvested populations and determining the viability of populations of conservation concern.

The method was also validated using empirical data. Aerial survey data were provided for 16 MMAs that included areas in both the north and south of Sweden. The aerial surveys were conducted between 2011 and 2012 and density estimates were obtained using the Distance sampling method (Thomas et al. 2010). We compared density estimates from the aerial surveys with those derived from the harvest data (see section 2.6) using our simplified method. A simple linear regression is used to describe the relationship between the density estimates and their correlation is reported using the R^2 statistic.

2.7.4 Paper VI

Paper VI explores the relationships between vegetative productivity, moose density and predation under the predictions of the exploitation ecosystems hypothesis. However, we explore this in a system where human hunters are the main predator, which means that moose predation (i.e. harvest rates) can be quantified throughout the country. Vegetative productivity was measured using dynamic habitat indices (Table 1) and habitat variables were also included to measure how habitat suitability may also influence harvest rates. We fitted linear regression models to test the relationship between harvest rates, vegetative productivity and habitat. However, some variables were highly correlated so we used sequential regression to correct for collinearity. Sequential regression uses the residuals of two correlated explanatory variables as a new explanatory variable (Dormann et al. 2013). We first identified the

most important variable in the linear model, i.e. the variable with the highest independent contribution, which was determined using hierarchical partitioning (MacNally 1996). The second most important variable was then regressed against the first, and the residuals of this regression represent the independent contribution of the second variable after accounting for the first variable (Dormann et al. 2013). The top performing model was determined by AICc (Burnham and Anderson 1998) and the predictive accuracy of the model was determined through ten-fold cross validation (Kohavi 1995).

The second part of the paper investigated how moose densities (per $10km^2$) correlated with vegetative productivity. Moose densities had been estimated using the method described in Paper V. The EEH predicts herbivore densities to be stable across productivity gradients, whereas herbivore densities may explode in the absence of predation (Oksanen and Oksanen 2000, Ripple and Beschta 2012, Letnic and Crowther 2013). This has been shown in ungulates by comparing herbivore densities in areas with and without predation, for example predation by wolves (Ripple and Beschta 2012). We adopted a similar approach and classified each MMA has having “Low”, “Intermediate” or “High” harvest pressure. Harvest pressure was calculated by dividing density by harvest rate, and then dividing the result into quartiles. The interquartile range was “Intermediate” harvest pressure. We used multiple regression to compare the relationship between moose density and the DHIs under these differing categories of harvest pressure. We identify whether the correlation between density and vegetative productivity was significant, and whether the slopes of the relationships were significantly different from each other.

3 Results

3.1 Paper II – Methodological Guidance

A number of factors were found to influence the performance of the NSD model in both classifying and quantifying movements. Careful consideration should be given to individuals classified as mixed migratory, i.e. individuals showing a migratory pattern but return to a different location than where they started. Individuals may return to an area that is within the bounds of normal home range movements (e.g. 1km radius from starting location) but this may still be classified as mixed migratory. Individuals may also move to areas that are further away, i.e. showing an increase in NSD, yet the model may still classify this movement as mixed migratory when it would normally be considered as a dispersal movement.

The extent of movements influenced the accuracy of the classification of an individual's movement strategy (Figure 5). The majority of movements that were incorrectly classified as migratory had an extent that was less than 10 km (Figure 5). Movements that were incorrectly classified tended to have poorer model fits (mean = 0.50, sd = 0.23) compared with correctly classified individuals (mean = 0.89, sd = 0.12; Figure 5).

In terms of quantifying movements and extracting the distance, timing and duration of movements, the starting date of a trajectory had a minor impact on parameter estimates. For moose, trajectories should not start in June, December or January since migrations have begun during this period and it is thus quite likely that an individual may be between seasonal ranges. The optimal start date for quantifying the spring migration is between February and May, and between August and November for the autumn migration.

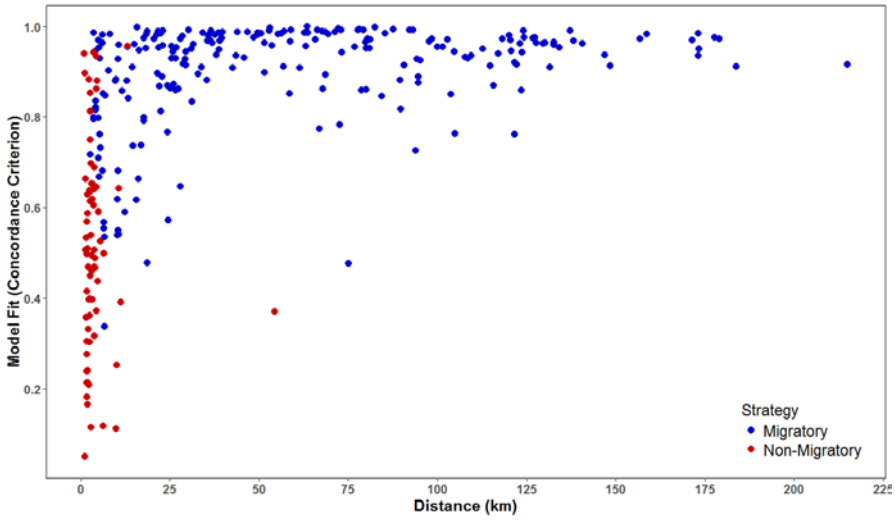


Figure 5 *– The model fit (Concordance Criterion; CC) in relation to the extent of movement for individuals classified as migratory using the NSD method (n = 299). Solid points indicate individuals correctly classified whereas hollow points were individuals incorrectly classified as migratory. Misclassified individuals tended to have smaller scales of movement (<10km) and lower CC scores (<0.7).*

The treatment of the starting location also influenced parameter estimates. Using a harmonic mean location during the first month generally improved model fit (i.e. higher CC scores), and parameter estimates for the distance and timing of migrations were more accurate. This was particularly evident during autumn when a mean location had the effect of smoothing erratic movements during the rutting period. Using a mean location during the first month also reduced the risk of using a location from an exploratory movement and thus provided a more accurate NSD curve (Figure 6).

The resolution of the data also impacted the performance of the NSD models. Model convergence was near impossible to achieve with high resolution data (i.e. 48 locations per day). The reason is the sheer quantity of data points to which the model was being fitted to. This resulted in more simplified models which had a strong negative impact on the estimates for distance, timing and duration. Instead, a single location per day, or a mean location per day, is more appropriate for modelling migration.

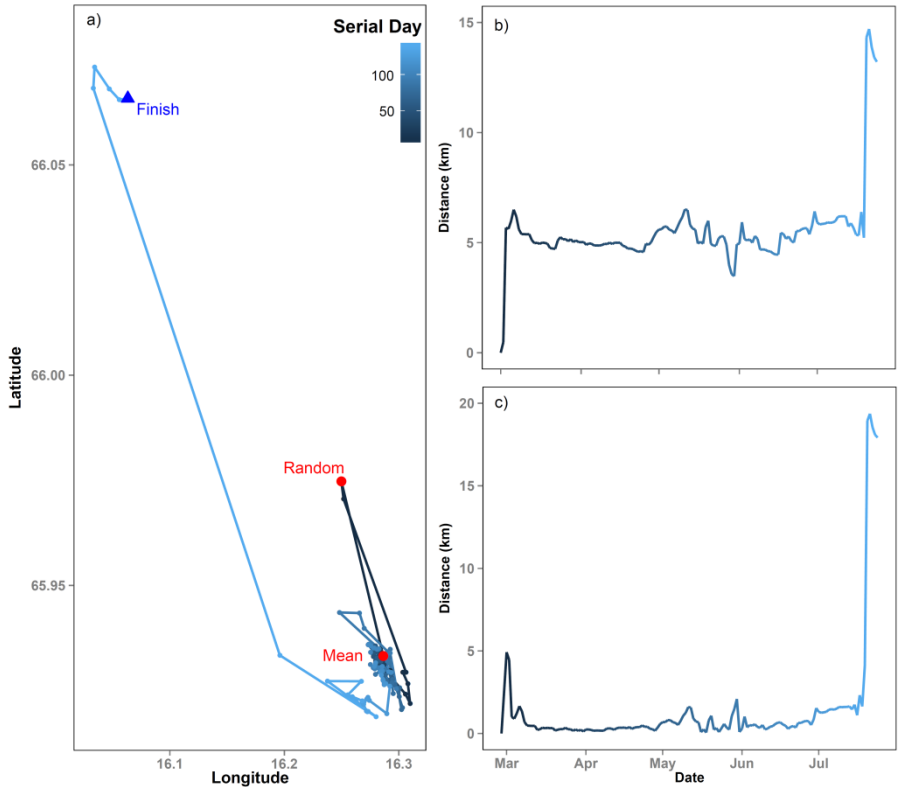


Figure 6 – *The effect of using a random or mean starting location, a) shows the trajectory of a movement starting in March and ending in July where both a random starting location (the first location in a trajectory) and a mean location during the first month are shown in red, b) shows the net-squared displacement (NSD) using the random starting location and c) shows the NSD using the mean starting location.*

3.2 Paper II & III - Movement Classification and Quantification

The majority of movements were classified as either migratory (50%) or sedentary (48%) with only 1% classified as dispersal and <1% as nomadic. There was a clear north-south divide in the type of movements, with the five northern study areas dominated by migratory individuals and the five southern areas dominated by sedentary individuals (Figure 7). However, there was variation in the proportion of movement types in most populations which provide clear indications of the partially migratory nature of moose in this region. Three populations do not appear to exhibit partial migration with nearly

100% of sampled individuals classified as migratory in N5 (1 individual was classified as dispersing) and 100% of sampled individuals classified as sedentary in S2 and S5 (Figure 7).

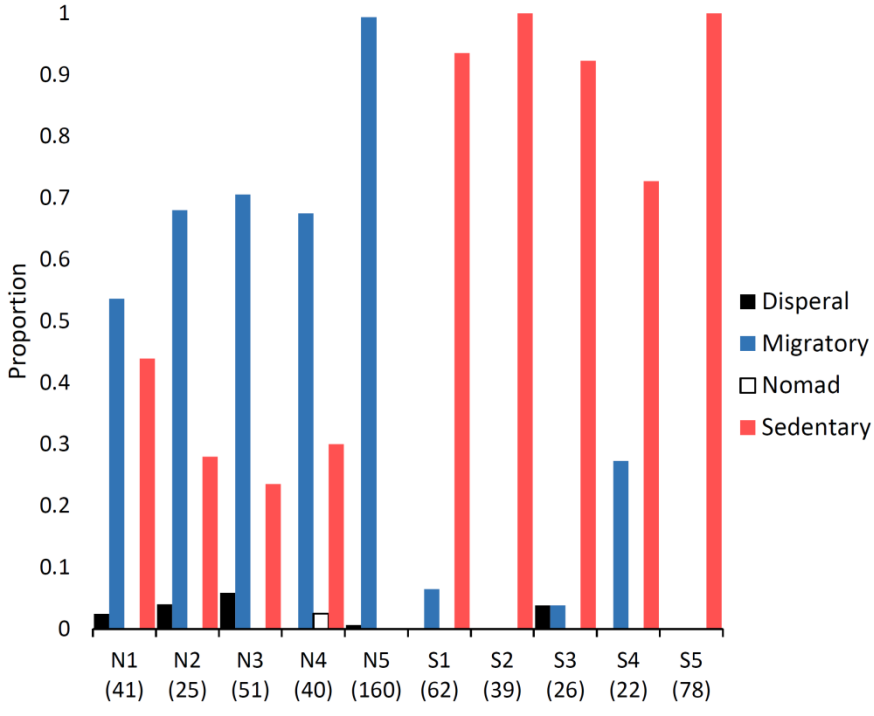


Figure 7 – *Classification and proportion of movements in the five northern and five southern study areas (see Figure 3). The number of annual trajectories is shown in brackets below each study area and signifies the sample size of Paper III, with a total of 544 annual trajectories.*

The extent of migrations varied widely across individuals and populations. Migrations were rarely in excess of 10km in the southern populations but the mean migration distance ranged from 30 – 45 km in N1 to N4 and nearly 90 km in N5. The longest recorded migration was 212 km, giving a round trip distance of approximately 425 km. Most individuals in the northern study areas arrived at the summer range in early June with the spring migration lasting approximately three weeks (Figure 8). Most individuals in the northern study areas left the summer range in late November, with the autumn migration taking nearly five weeks, and individuals tended to arrive back at the winter range in late December (Figure 8). The mean arrival date in the summer range

coincided with the start of the growing season and most individuals left the summer range long after snow depths were >5 cm (Figure 8).

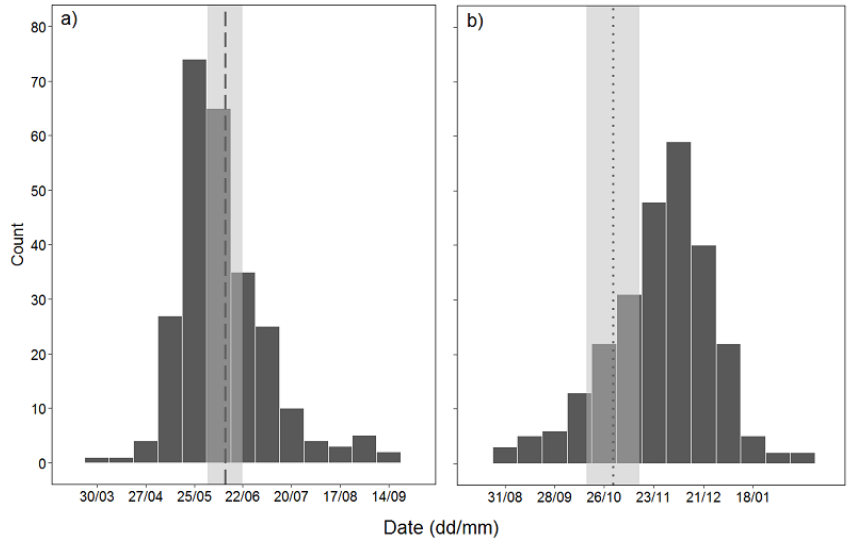


Figure 8 – *The timing of migrations in N3, N4 and N5 for moose arriving at the summer range (a) and leaving the summer range (b). The dashed line (a) indicates the mean start date of the growing season (12 June) and the dotted line (b) indicates the mean date that snow depths are greater than 5cm (26 October). The shaded regions illustrate the standard deviation around these dates.*

3.3 Paper III - Home Ranges

Home ranges varied significantly among individuals, populations and seasons. In all northern study areas, and in S1 and S2, the summer home range was significantly larger than the winter home range (Figure 9). Interestingly, the winter home range was significantly larger than the summer home range in S4. The largest summer home ranges were in the northern study areas whereas the largest winter home ranges were in the southern study areas, namely S3 and S4 (Figure 9). When considering variation in home range size among populations, study area alone explained 55% of variation in summer home range size and 24% of variation in winter home range size. Variation in summer home range size among populations was explained by variation in vegetative productivity (NDVI), available energy (growing degree days) and elevation. Home ranges were smaller in areas with higher vegetative productivity and available energy whereas they were larger in high elevation areas, and these variables explained 52% of variation in home range size. Models explaining variation in winter home range size among populations tended to perform poorly, and the top model had a ΔAIC of 0.54 compared to a NULL model and only explained 3%

of variation in winter home range size. This model included snow depth and the density of moose, with home ranges decreasing in size as snow depth and moose density increased.

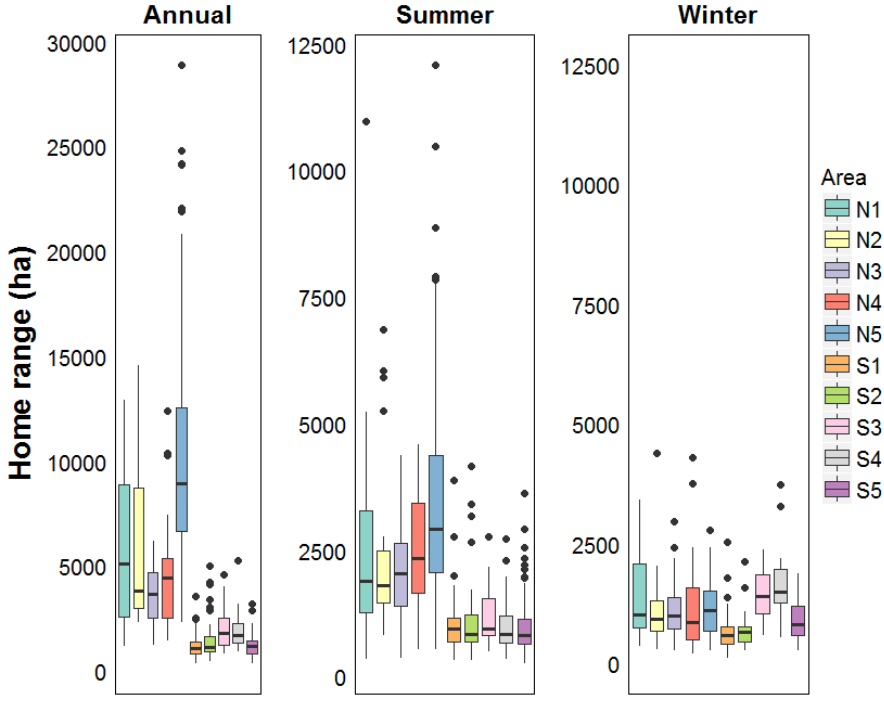


Figure 9 – *Annual, summer and winter home range size for the ten study areas. The boxes show the interquartile range (IQR; 25% - 75%), the solid line shows the values within 1.5*IQR and solid points are the outliers.*

A number of factors were found to cause variation in home range size among individuals in the same population. Few populations showed similar characteristics during summer although broad trends were apparent from the results. The life history traits of an individual were more important in southern than northern populations, whereby males had larger home ranges and older individuals had smaller home ranges on average. The structure of the landscape was more important for explaining home range size in northern study areas, with home range size increasing as the landscape became more heterogeneous. Increasing proportions of poor quality habitats like mires and thickets resulted in larger home ranges in the north, whereas high quality habitats like clear-felled areas were more important in the south, and increasing proportions of these resulted in smaller home ranges on average. During winter, factors affecting home range size were more comparable across northern and southern

populations. Forested habitats and areas with higher NDVI levels during winter resulted in home ranges that were smaller on average. Age was also important in several areas and older individuals had smaller home ranges. Snow depth was only important in some of the northern study areas where increasing snow depth resulted in smaller home ranges. The lack of its importance in the south is likely due to snow depths not reaching critical levels (>70cm; Sweanor and Sandegren 1989) in southern study areas.

Again I will reiterate that a number of factors were found to influence home range size among individuals. I have only provided a broad summary of the 24 models in the results here, and to fully appreciate which factors influenced home range size I would encourage interested readers to view the results of Paper III.

3.4 Paper IV – Habitat-Performance Relationships

During the study period of Paper IV, there were 29 calving events and 16 occasions that a female did not reproduce. Of the 29 calving events, 15 were twins meaning a total of 44 calves were born during this period. There were four females that did not give birth during the entire study, but the ages were evenly spread (2, 5, 9 and 15). The calving rate of females did not vary between females that had lactated the previous year and those that had not. Fecundity rates did appear to be affected by a female's space use patterns though, with increased use of broadleaf forest in the summer prior to parturition resulting in higher fecundity ($P = 0.04$). The time spent in arable land in the summer prior to parturition may also have a negative impact on fecundity ($P = 0.051$, $\Delta AIC = 0.28$).

Calf survival was low across all years compared to other regions of Sweden, with survival rates of 0.36 (se = 0.13) in 2012, 0.05 (se = 0.05) in 2013 and 0.46 (se = 0.19) in 2014. The majority of mortality events occurred during summer, i.e. after calving but before the hunting season started in the autumn. Calf survival did not appear to be affected by a carryover effect of females lactating the previous year. No female had 100% mortality of calves and only two females consistently raised a calf to the autumn, which may explain why including ID as a random effect did not improve model fit. The top three models explaining calf survival had R^2 values > 0.60 and had a ΔAIC less than 0.60. Females that spent more time in mixed forest habitats during winter had higher calf survival whereas time spent in thicket habitats reduced calf survival (Figure 10). Females with twins also had lower calf survival, as did older

females, but interestingly females that spent more time in mire habitats after parturition had higher calf survival (Figure 10). Mire habitats are not usually considered as preferred feeding habitats for moose (Bergström and Hjeljord 1987, Olsson et al. 2011), but our results, along with other studies, indicate that mires may have a nutritive value for females with calves (Paper IV; Bjørneraas et al. 2012). The most important variable in terms of explained variation (as measured by hierarchical partitioning) was the use of thicket habitats during winter, which contributed 33.6% of explained variation from a model set consisting of nine variables. The second most important variable was the use of mire habitats during summer which contributed 16.4% of explained variation.

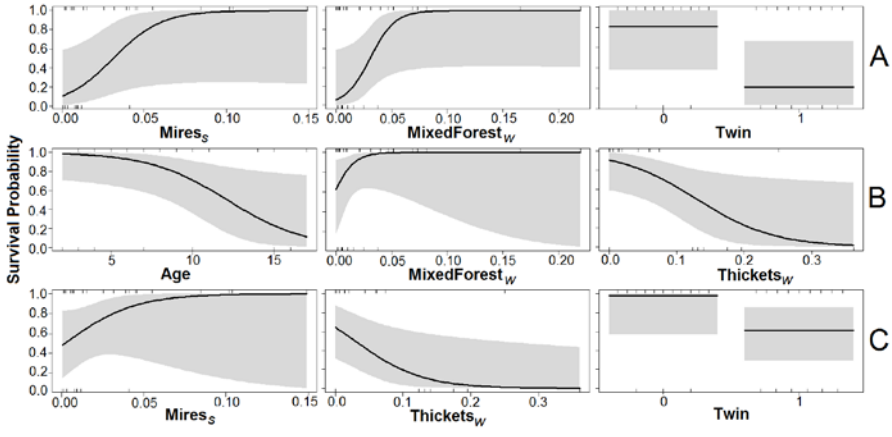


Figure 10 *– Modelled relationships of the top three models explaining calf survival, namely A: Mires$_s$ + MixedForest$_w$ + Twin, B: Age + MixedForest$_w$ + Thickets$_w$ and C: Mires$_s$ + Thickets$_w$ + Twin. The subscripts denote $_s$ = summer and $_w$ = winter. The shaded areas indicate the 95% confidence band.*

3.5 Paper V – Estimating Population Size

The performance of our simplified cohort analysis for estimating population size was encouraging when used on both the simulated and empirical data. The method accurately predicted population sizes produced by the individual-based population model (IBPM; Figure 11). Most results were within the 95% probability intervals and the method was also able to track a simulated increase and decrease in population size (Figure 11). The simplified cohort analysis assumes a stable population to estimate population size from age-structured harvest data, but our results indicate that this assumption may be relaxed somewhat when using the method. The precision of estimates increased as the sample size of aged individuals increased, with an average precision of 39%

when 25 individuals were aged compared to an average precision of 20% when 100 individuals were aged. Aggregating data across years appears to be a viable approach for increasing the sample size of aged individuals and aggregating data prior to running our simplified approach returned results with improved precision compared with using a moving average.

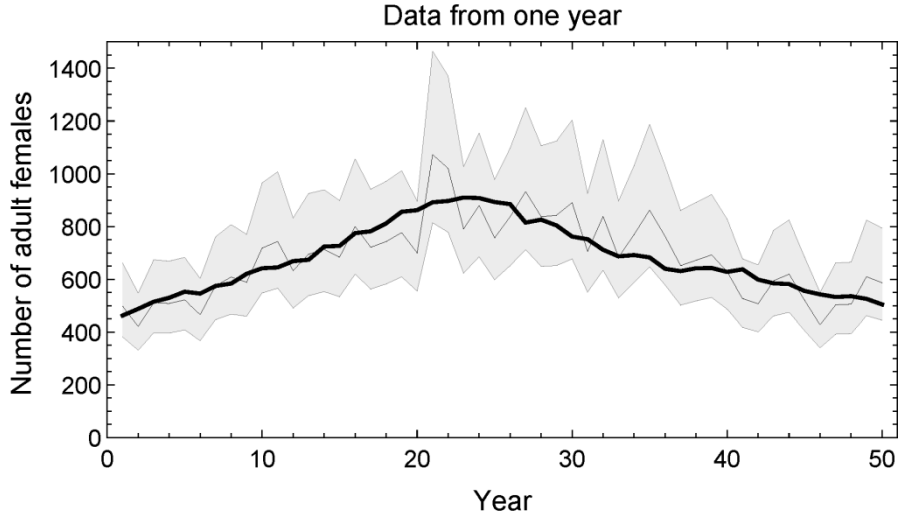


Figure 11 *- The cohort analysis is seemingly robust against population changes as long as the changes were not dramatic. Analyses based on 50 age determined individuals in an average cohort harvest of 234.*

Our simplified cohort analysis was also able to accurately estimate population size of empirical data. We found a strong correlation between the population size estimated by our approach and that of the aerial surveys (Figure 12). If the four largest populations were removed from the estimate, the slope of the relationship improved from 0.67 to 1.01 (Figure 12). Two of the MMAs that were under-estimated were areas with large proportions of migratory moose. Here it was important to consider how the density of moose may change in space and time. Our simplified approach measures density during summer (i.e. during the harvest period when moose are still in their summer ranges) whereas aerial surveys are traditionally conducted during winter when moose are aggregated in lower-lying coniferous forests. If the population estimates from Figure 12 are adjusted to account for this clumped distribution during winter, the two estimates become much more closely aligned (cohort analysis = 7,734, aerial survey improves from 12,008 to 8,405).

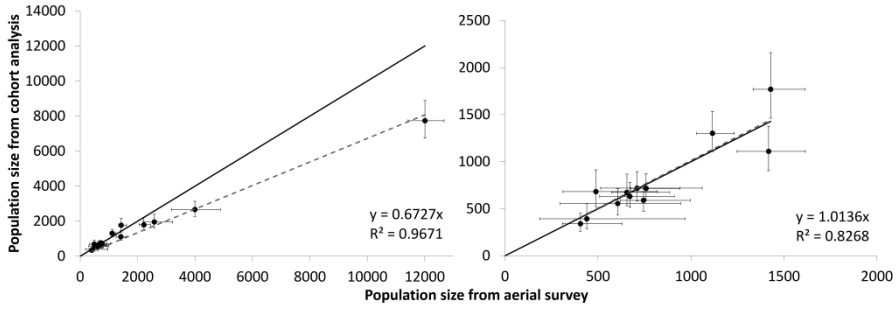


Figure 12 *- The correlation between the predicted number of moose from the cohort model and the estimated number of moose from the aerial surveys in a) all 16 areas and b) 12 areas with the lowest populations. The black line indicates a slope of 1, the dashed line is the linear regression of the points.*

3.6 Paper VI – Exploitation Ecosystems Hypothesis

Across all 147 MMAs, the variable within the dynamic habitat indices (DHI, containing data on cumulative annual productivity, minimum productivity and seasonality) that explained most variation in harvest rate was the seasonality of the environment ($P < 0.01$, $R^2 = 0.27$) and provided the best model fit compared with cumulative productivity ($P < 0.01$, $R^2 = 0.11$, $\Delta AIC = 29.23$) and minimum productivity ($P < 0.01$, $R^2 = 0.20$, $\Delta AIC = 14.66$). However, given our knowledge of how space patterns vary across the country (e.g. Paper II & III), we divided the MMAs into northern and southern areas, whereby the south included all MMAs south of Dalarna and Gävleborg (green and grey areas respectively in Figure 1). After this change, the strength of the relationship between harvest rates and productivity improved dramatically in southern MMAs, but instead of seasonality, minimum productivity had the highest correlation with an R^2 of 0.53. The northern MMAs had less correlation with the DHIs, and the DHI that explained most variation in harvest rates was cumulative productivity with an R^2 of 0.20.

The final model that explained harvest rates across all of Sweden included the explanatory variables of coniferous forest, minimum productivity, mixed forest and urban areas, and had an R^2 of 0.53 and $\Delta AICc$ of 1.95 over the next best model. The final model for the southern MMAs included cumulative productivity, minimum productivity, coniferous forest and urban areas, providing a final R^2 of 0.66. The final model for the northern MMAs did not

include any of the DHI variables, and instead the proportion of certain habitats in an MMA best explained variation in harvest rates. The habitats included in the final model were broadleaf forest, inland wetlands, mixed forest and urban areas, providing a final R^2 of 0.53. A consideration in the northern MMAs is the much larger size of MMAs and the large gradient in the environment from the coast to the mountains in the west. These large gradients were measured by a single value for the DHI and unfortunately, due to the way harvest data are collected, we could not measure these gradients at finer scales. The final models were able to predict harvest rates fairly accurately during cross-validation with a root mean-squared error (RMSE) of 0.632 in northern MMAs and 0.500 in southern MMAs.

The level of harvest pressure had a significant effect on the relationship between productivity and moose density. The slope of the relationship in areas with Low harvest pressure was significantly different from areas with Intermediate or High harvest pressure (Figure 13). Moose density and productivity were significantly correlated in areas with Low ($P < 0.001$, $R^2 = 0.49$) and Intermediate ($P = 0.03$, $R^2 = 0.06$) harvest pressure, whereas there was no correlation in areas with High harvest pressure ($P = 0.85$, $R^2 = -0.03$).

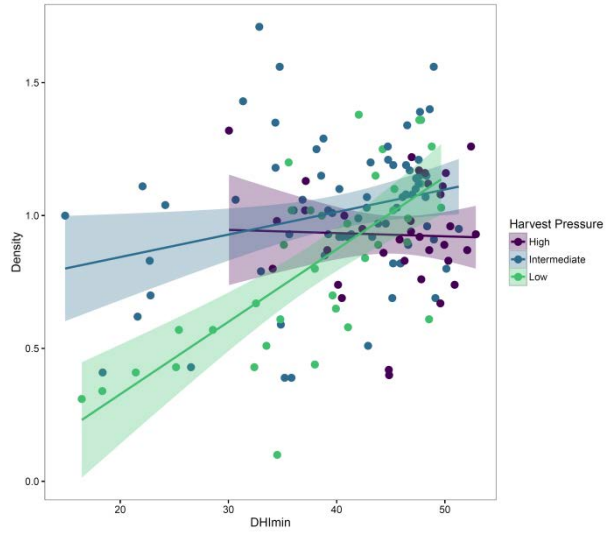


Figure 13 *– Correlation between minimum productivity (DHImin) and moose density (per 10km^2) for all MMAs in Sweden (n = 147). Harvest pressure was estimated by dividing density by harvest rates, and the categories were based on quartiles whereby the interquartile range was classified as Intermediate. The shaded areas indicate the 95% confidence bands.*

4 Discussion

My dissertation provides a framework for linking movement ecology to the management and conservation of mobile species. As I detail in Paper I, the knowledge gained from movement ecology may be vital for identifying novel and improved methods of wildlife management. Several methods recently described in the literature depend explicitly upon knowledge of species movements. These include spatial management units that shift in space and time (Game et al. 2009, Singh and Milner-Gulland 2011a), conservation actions that are targeted at specific movement phases (Hunter et al. 2006, O'Neal et al. 2008, Shillinger et al. 2008) and an understanding of not only which habitats animals need to move (Dennis et al. 2013, Squires et al. 2013), but also identifying how movement may be impeded in future (Sawyer et al. 2013, Seidler et al. 2015). These thoughts have guided the development of my dissertation and initially I will reflect more broadly on the research I have performed and how this relates to science, management and conservation of mobile species in general. I will then return to the specific objectives of the dissertation in regard to managing moose in Sweden.

The rapid advances in tracking technologies place us in an exciting era of animal movement discoveries. Yet, it would seem that for every new article describing a species' movement ecology, there is also a new article that describes a novel method for analysing movement data. Formerly managers and practitioners would consider minimum-convex polygons or slightly more advanced kernel approaches. The method I used in this dissertation of biased-random bridges were new and novel when I began, but home range analyses now incorporate autocorrelated kernel density estimators (Fleming et al. 2015), develop mechanistic approaches for optimally estimating home ranges of territorial species (Tao et al. 2016) or elliptical time density models for estimating utilisation distributions (Wall et al. 2014). Often these methods require detailed statistical knowledge, specific software to implement the

analyses and may even lack information about how the method can be implemented. Although it can be said that these methods raise the standard of science, they also reduce the accessibility and usability for less statistically-minded ecologists and practitioners and may introduce unnecessary complexity (Murtaugh 2007). However, it almost becomes a requirement to use the latest methods, as an example, a reviewer stated that the Manly's selection ratios (Manly et al. 2007) I had used were too basic given the alternative options available for analysing habitat selection today.

The suite of new methods for analysing animal movement raises a number of challenges that need to be addressed. For example, are traditional methods still ecologically meaningful (in my above example apparently not according to the reviewer), which method should be used and how can they be implemented? One solution is to strengthen collaborations between scientists and practitioners, a call that has already been re-iterated among several fields of ecology (Knight et al. 2008, Cook et al. 2013, Hulme 2014, Walsh et al. 2015), or that scientists should implement the management actions themselves (Arlettaz et al. 2010). A consideration is the time scales of interest though, a manager has a long-term vision for managing a species whereas scientists often have shorter-term goals regarding specific projects or funding proposals, and thus operate on different time scales to managers and practitioners. To reduce managers' reliance on scientists, methodologies need to be tractable and authors should provide guidance for how others may implement the methods themselves. The increased use of freely available software like R (R Development Core Team 2012), and the ability to provide code used in analyses, is one step towards achieving this. These considerations are what drove us to write Paper II. We saw the value of the NSD method in not only classifying movements but also quantifying these. The NSD method also performs well in comparison to overlap indices and clustering approaches (Cagnacci et al. 2016) and thus could be a useful addition to managers' methodological toolbox. As I outlined earlier, several management approaches require knowledge of the timing of movements which is knowledge that can be provided by the NSD method. Hence our goal was to improve the usability of the approach, especially considering that analysing movement data is a pre-requisite for implementing the movement-management framework.

The first step of the movement-management framework in Paper I seeks to understand the movement attributes of the species. This connects back to my introductory paragraph of knowing enough about a species to achieve a management goal (Fryxell et al. 2014). Paper III and IV in particular aim to

improve our knowledge about a species' movements. Understanding intra-specific variation in space use patterns (Paper III) has a number of implications for wildlife management. As stated earlier, home ranges are commonly used as a scaling factor for wildlife management (Schwartz 1999) and understanding what causes variation in home range size will enable managers to determine optimal scales of management across different landscapes. Managers also need to be aware of how species may respond to human-induced change, such as climate change and landscape change (Fahrig 1997, Walther et al. 2002, Ewers and Didham 2006). Paper III illustrated how the effect of environmental factors varied within and among populations. Vegetative productivity had a strong influence on the scale of movements, and as the climate changes and leads to an expected increase in productivity (Nemani et al. 2003), how may this influence population-level movements? Factors that are important for managers to consider may also vary among populations. Future land-use change may have a greater influence on the population-level movements of one area than another. In Paper III, landscape heterogeneity was generally the most important variable for explaining variation in home ranges in the north and therefore land use change may have a greater influence on population-level movements. Meanwhile, the life history traits of an individual were generally more important in southern populations, and management actions like sex or age-biased hunting may have a greater influence on southern population-level movements.

Paper III also provides insights about scaling up observations taken from a few individuals to derive population means. Few studies have been able to analyse intraspecific variation in space use patterns at this scale, both in terms of the large geographical gradient and the number of individuals included in the study. Paper III, along with other studies conducted at similarly broad scales like Morellet et al. (2013) and Walter et al. (2009), have highlighted how broad scale factors related to climate influence home range along with fine scale factors like the landscape structure and life history traits of the individual. Understanding how these factors interact to produce the observed space use patterns is paramount to predicting population-level movement patterns.

Paper IV also investigated intraspecific variation in space use patterns but the goal was to understand how this influenced individual performance. The detailed information provided by GPS collars has enabled researchers to investigate how an individual's movements influence their performance, i.e. habitat-performance relationships (Gaillard et al. 2010, Morales et al. 2010). Paper IV provided a strong indication of a habitat-performance relationship,

particularly habitats used in the winter prior to parturition. Understanding what influences a species demography is vital for developing management and conservation plans (Fryxell et al. 2005, Taylor et al. 2012). This has become apparent for managing moose on Öland as well, since a previous management plan assumed recruitment was much higher than it actually was (Jonsson 2007), and thus failed to meet the harvest goals set out in the management plan. In addition to understanding direct habitat-performance relationships, further research is also needed to understand how climate change may interact with habitat-performance relationships (Middleton et al. 2013, Monteith et al. 2014). We observed an advance in the growing season of nearly three weeks, which may create a mismatch between the periods of greatest energy demand and forage quality (Post and Forchhammer 2008, Miller-Rushing et al. 2010), but unfortunately we lack the longitudinal data to determine how the timing of parturition has changed during this time. Climate change is also likely to increase exposure to parasites (Kutz et al. 2004, Malmsten et al. 2014) and induce heat stress, which increases energy demands for thermo-regulation (Lenarz et al. 2009, van Beest et al. 2012). These climatic effects may not only have direct impacts on performance, but also indirect impacts through for example behavioural responses to temperature that lead to altered habitat-use patterns (van Beest and Milner 2013, Melin et al. 2014).

Returning to the movement-management framework, Paper III and IV have provided an overview of the types of movement in the population, the scale and timing of migratory movements, details of the home range and factors that influence these, and how this may influence population demographics. These are directly related to identifying the scale of management. Paper V also provides an important contribution for identifying the scale of management and is related to the implementation and evaluation of management actions as well (Figure 2). Monitoring population size is an essential component of managing a harvested species (Yoccoz et al. 2001, Bunnefeld et al. 2011b) and for conserving species too (Noss 1990, Fryxell et al. 2014). The importance of estimating population size is evident in the suite of methods available (see for example Schwarz and Seber 1999, Bibby 2000, Wilson and Delahay 2001, Sutherland 2006), and similarly a number of methods have been developed for monitoring harvested ungulates (Rönnegård et al. 2008, Singh and Milner-Gulland 2011b, Ueno et al. 2014). Most methods have some form of compromise between accuracy, cost or spatial coverage (Rönnegård et al. 2008, Månsson et al. 2011). My hope is that Paper V overcomes several of these challenges and that the simplified approach (i.e. relaxed assumptions and reduced statistical detail) improves usability for managers and practitioners.

The simplified approach of Paper V for estimating population size proved to be accurate, and precise, when compared to both simulated and empirical data. The method requires a minor behaviour change, and calls on hunters to act as citizen scientists by collecting age data. In that way data collection would be low cost and hunters in Sweden are already actively involved in monitoring schemes (Singh et al. 2014), with some already reporting age data. Therefore, I do not envisage much opposition to increasing the level of aging that is currently done, especially if it aids population management. Age can be determined fairly accurately for moose and Rolandsen et al. (2008) found that even untrained technicians were able to age moose relatively accurately. Paper V also demonstrated how the harvest data can be scaled up or down, which not only overcomes challenges of identifying monitoring methods with appropriate spatial coverage, but it may also help determine the spatial scale of management. The performance of the method depended somewhat on the number of aged individuals, and for example MMAs could be combined to achieve the required level of detail for accurate population estimates. Paper V identified that 11% of MMAs may be too small for implementing the method. In contrast, a number of areas were larger than necessary for accurately estimating population size, but here it is important to consider animal movement since these areas also contained larger proportions of migratory individuals.

Paper VI provided the opportunity to evaluate the role of hunters under the theoretical framework of the exploitation ecosystems hypothesis (Oksanen et al. 1981, Oksanen and Oksanen 2000), and to link this in an applied manner to wildlife management. Typically, the EEH has been explored at localised scales where the environment may for example be manipulated through exclosures or through the use of fertilisers (Olofsson et al. 2002, Gough et al. 2012). Alternatively, larger scale studies often use information on herbivore biomass and relate this to productivity (Crête 1999, Ripple and Beschta 2012, Letnic and Crowther 2013). Paper VI used a novel approach because we were able to estimate predation across a large geographical scale. The reason is that large predators have been largely extirpated and therefore hunting is the principle cause of mortality of moose in northern Europe (Solberg et al. 1999, Ericsson and Wallin 2001). We also wanted to understand how moose density correlated to vegetative productivity. According to the EEH, herbivore densities are fairly stable across productivity gradients. But when released from predation, herbivore densities may explode, which has been observed in areas with and without wolves (Ripple and Beschta 2012) and dingoes (Letnic and Crowther

2013). Understanding the interaction between productivity, herbivore density and predation is important for preventing trophic cascades. Trophic cascades have been reported in a number of ecosystems today, where herbivore populations have grown exponentially following the persecution of large carnivores (Terborgh 2001, Estes et al. 2011, Ripple et al. 2014). Preventing trophic cascades requires an understanding of the level of population control needed to maintain a stable population. Paper VI provided the opportunity to evaluate whether human hunters mimic predators, and if they fulfil their role in controlling herbivore populations.

We found a significant correlation between harvest rate and vegetative productivity, thus supporting the general predictions of the EEH. This relationship was even stronger in the south where the environment is less seasonal and moose are more sedentary. We also found that the level of harvest pressure had a significant impact on the relationship between moose density and vegetative productivity. We found no relationship between density and productivity in areas that were categorised as having a high harvest pressure. However, we found a positive and significant correlation between moose density and productivity in areas with low harvest pressure. A couple of observations could be noted though, the first is that the density of moose in areas with high harvest pressure was higher than one would expect (Figure 13). If hunters fulfilled their role as a carnivore, then the density should actually be nearer the levels seen in areas with low vegetative productivity. This is probably an indication of management interventions on the landscape, and for example the management objectives in these areas may aim to maintain densities at higher levels to support the annual moose hunt.

The trends observed in areas with Low harvest pressure also support the concept of herbivore populations exploding in the absence of predation and has been reported previously, for example Ripple and Beschta (2012) and Letnic and Crowther (2013). Managing the impacts of herbivores is important for preserving biodiversity and ecosystem functions. Our approach may provide some important tools for managers, for example we were able to identify areas that harvested more or fewer individuals than expected given the observed productivity. Paper VI was conducted at a very broad scale of MMAs, but to increase its usability for management, further work is needed if we are to spatially prioritise management actions based on vegetative productivity. Together, Papers II – VI have yielded a number of insights regarding managing moose in Sweden and understanding the scale at which to manage moose.

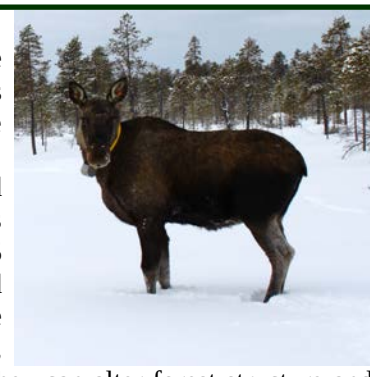
4.1 Moose Movement-Management Framework

My dissertation has provided me the opportunity to develop a conceptual framework for managing mobile species, and to address different topics regarding species ecology and wildlife management. At the same time, I have specifically focused on the moose management system in Sweden in the hope that the knowledge generated in this dissertation may contribute towards moose management. In the next section, I use the results of my dissertation, along with other research on moose, to describe the movement-management framework for moose. Box 2 presents the movement-management framework outlined in Paper I. The diagram has been completed specifically considering moose movement ecology and management, and Box 2 also includes a summary of managing moose in Sweden. I expand on each of these sections in detail in the text below, including the management goals, movement data and the five steps of the movement-management framework (Box 2; Figure 2).

4.1.1 Management Goal

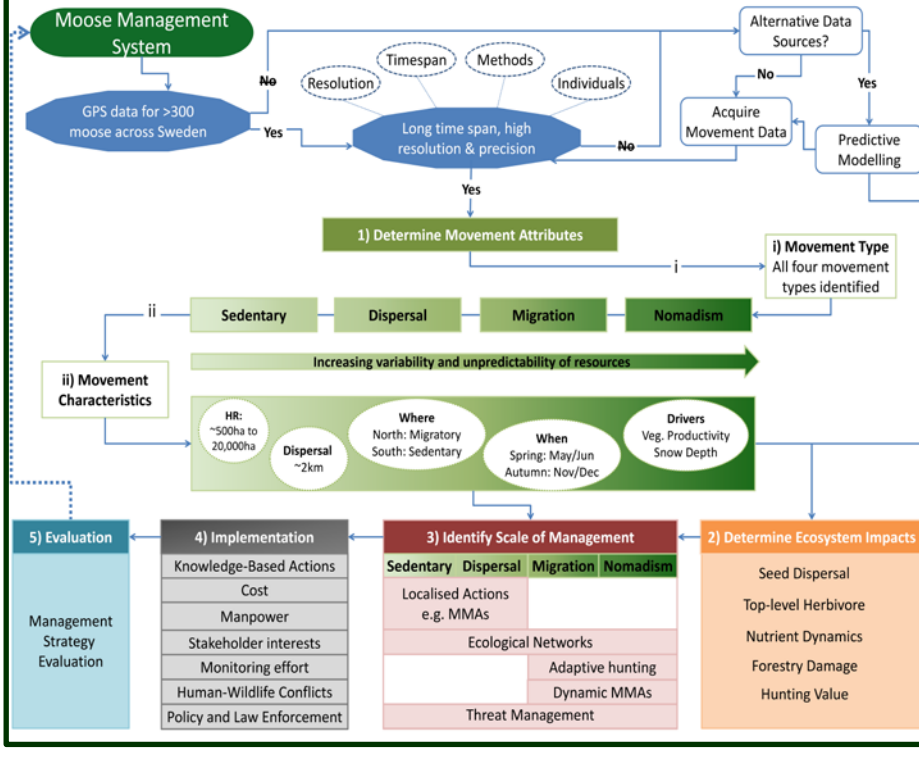
The objectives of moose management in Sweden are to sustain a healthy population that is in balance with food resources and takes into account the interests of numerous stakeholders, such as traffic, agriculture, forestry, hunting, the general public and impacts on biodiversity. McGowan and Possingham (2016) expanded upon the movement-management framework described in Paper I, by highlighting the need for quantifiable objectives and to determine whether movement data would provide an improvement to wildlife management. Determining these quantifiable objectives for moose would require additional research to identify appropriate levels of management intervention. The principle management action is the moose harvest, therefore a quantifiable goal would be to achieve a desired harvest rate that sustains a stable population. Quantifiable objectives may also include a maximum percentage level of browsing damage to Scots pine, and a maximum number of vehicle accidents per year. Adjustments to harvest rates will have knock on effects to browsing damage and traffic collisions, hence the need for more research to identify optimal harvest rates. McGowan and Possingham (2016) question the value of obtaining more movement data and suggest that managers need to consider the value of information (VOI; McGowan et al. 2016). They argue that there may be little return on investment when tracking animals, especially as there are few examples of animal tracking informing conservation decision making (McGowan et al. 2016). I agree this may often be the case and which is why I encourage a stronger link between the fields (Paper I). I would however argue that understanding a species movements increases the number of management actions that can be included in the decision making process. In

Box 2 – Managing moose in Sweden



Multi-year high precision GPS data is available for >300 individuals. The movement type was classified as predominately migratory in the north compared to sedentary in the south. Areas utilised were ~1,444 ha in the south and ~7,300 ha in the north. Migratory distances were up to 212 km but averaged between 35 km and 80 km. Spring migrations occurred during May/Jun and autumn migrations were during Nov/Dec. Moose disperse seeds, transfer nutrients and as top-level herbivores they can alter forest structure and succession. The sedentary movements in the south allows for a more static approach to management which is guided by the scale of movement and desired population densities. However, the long distance migrations of moose in the north need alternative management approaches to incorporate these movements. This could include a combination of static areas for managing sedentary moose along with larger areas that incorporate the migratory movements of moose. The spatial uncoupling of management action from management goal (i.e. hunting during summer, forest damage during winter) requires a more adaptive approach to hunting. These issues are expanded up in the main text of the dissertation.

Photo: Andrew M. Allen



addition, movement data are already available for a number of species, including moose, and managers should maximise returns from investments that have already been made. In this instance, it would appear that tracking moose has a high VOI since the complex movements of moose are explicitly mentioned in the moose management system, and that improvements are needed to match the scale of management with the species movements.

4.1.2 Movement Data

The moose has been the subject of long term tracking studies. VHF collars were used in the late 20th century which gradually moved over to GPS collars in the 2000s (Ball et al. 2001, Singh et al. 2012). Movement data are available across a wide latitudinal gradient in Sweden which has allowed in-depth studies of their movements and how these impact management objectives (Singh et al. 2012). The movement studies in this dissertation (Paper II – IV) draws on movement data from more than 300 individuals. Knowledge can also be drawn from a number of other movement studies conducted in northern Europe (e.g. Bjørneraas et al. 2011, van Beest et al. 2011, Melin et al. 2014) and North America (e.g. Ballard et al. 1991, Testa et al. 2000, Lenarz et al. 2009).

4.1.3 Step 1 – Movement Attributes

The moose is partially migratory, with predominately sedentary movements in the south compared to predominately migratory movements in the north (Paper III; Ball et al. 2001, Singh et al. 2012). Migratory distances vary from just a few kilometres to over 150km (Paper II and III). The bulk of spring migrations are during May/June and of autumn migrations during November/December (Paper II and III; Singh et al. 2012). Studies of dispersal are few but indicate that natal dispersal occurs approximately one year after birth and dispersal distance is approximately two km (Cederlund et al. 1987, Labonte et al. 1998). Annual home ranges are smaller in the south ($\bar{x}$ = 1,444 ha) than in the north ($\bar{x}$ = 7,300 ha; Paper III). Similarly summer home ranges are smaller in the south ($\bar{x}$ = 1,054 ha) than the north ($\bar{x}$ = 3,009 ha) whereas winter home ranges are more comparable in size (south = 912 ha, north = 1,199 ha; Paper III). Movement patterns are influenced by inter alia life history traits, vegetative productivity, landscape composition and precipitation (Paper III, Ball et al. 2001, Singh et al. 2012). These factors may also influence the performance of individuals and for example the increased use of sub-optimal habitats may reduce reproductive performance (Paper IV; Milner et al. 2013).

4.1.4 Step 2 – Ecosystem Impacts

Moose connect habitats in space and time with genetic material, transport nutrients or seeds and are preyed upon (Pastor et al. 1993, Lundberg and Moberg 2003). Moose can decrease nitrogen mineralisation and net primary productivity through selective foraging of species which may influence commercial forestry (Pastor et al. 1993, Edenius et al. 2002). Moose may also impact ecosystems if the population is mismanaged and becomes overabundant. Over-browsing by large ungulates may reduce habitat quality and decrease forage resources for other species like songbirds (Allombert et al. 2005, Rae et al. 2014). These effects may also be localised due to the use of feeding stations, and the impacts may vary across functional groups such as insect or seed eating birds (Mathisen and Skarpe 2011). Moose are an important resource for hunters for recreation and meat (Ljung et al. 2012). However, moose also have a detrimental economic impact caused by browsing damage to commercially important forest species, such as the Scots pine and birch spp. (Danell et al. 1985, 1991). Finally, moose impact the general public, both through the aesthetic value of seeing moose in the wild and the detrimental effects of wildlife-vehicle collisions (Rolandsen et al. 2011).

4.1.5 Step 3 – Scale of Management

The variability in the movement patterns between the north and the south of Sweden highlight why it is important to incorporate movement into management planning. Moose in the south are largely sedentary with mean annual home ranges of ~1, 500 ha (Paper III). Although home range sizes are variable, understanding the environment and landscape structure would improve predictions of home range size at finer scales (Paper III). Hunting strategies may also have a strong and long-lasting influence on sex and age ratios (Sylvén 2003), which would also influence space use patterns of moose (Paper III). The scale of management for setting hunting quotas would be guided by the mean home range size and the desired population size within a management area. In the south, MMAs are smaller and therefore management actions are more localised. The primary stakeholders consisting of hunters and foresters will occur within the same management area, thus negotiations can be held to identify threshold levels for moose density and subsequent browsing damage. These negotiations could identify trade-offs, such as acceptable forestry losses which may be compensated through the benefits received by the hunter (Redpath et al. 2013). This system is not unlike the existing management system today, whereby the management boards of MMAs consist of representatives for different stakeholder groups. However, as we highlight in Paper V, some of the MMAs in the south may be too small to achieve desired

monitoring outcomes, which are important considerations for implementation (Step 4, Box 2) and management strategy evaluation (Step 5, Box 2).

Future management actions would also need to consider the connectivity in the landscape to maintain dispersal movements and thus genetic diversity and population viability. These management actions would focus on finer scales of management than the MMA, and for example could be implemented by land owners or hunting teams. The goal would be to create an ecological network that maintains connectivity of moose populations, and thus gene flow, nutrient transfer and other ecosystem processes. The population density of humans is higher in the south, thus issues regarding connectivity may be of greater importance compared to the north. In the south, the landscape is also more fragmented between forestry and agriculture, along with a greater number of roads and fenced highways (Figure 4). Thus, further research would be needed as to whether wildlife crossings on roads achieve their purpose, and whether the fragmented landscape creates a barrier to moose movement. Early indications are that fenced highways in particular are restricting movements in the landscape, along with migratory movements of moose as well (Seiler et al. 2003, Bartzke et al. 2015)

A different approach would be required for management of northern moose populations. Moose in the north are predominately migratory, often migrating in excess of 100km (Paper II and III), thus upscaling the scale of management is required. Currently, MMAs in the north are larger and have been designed to include the annual movements of moose into a single MMA (Figure 14). However, it is clear from Figure 14 that moose regularly traverse across MMAs and even across national borders. From our sample of GPS-collared moose, 25% of moose traversed across at least two MMAs and 16% across national borders. If I narrow the focus to Västerbotten, 30% of moose are traversing across at least two MMAs and approximately 40% of tracked individuals were moving between Norway and Sweden. Naturally these estimates reflect the percentage of moose in the regions we have monitored (Figure 14). Changing existing MMA boundaries, for example, establishing management boundaries by watersheds rather than administrative boundaries may improve the spatial scale of management. Alternatively, MMAs need to ensure clear and transparent communication so that management actions are shared among MMAs. In addition, communications are needed between Norway and Sweden to establish transboundary-boundary collaborative management actions of the shared moose population (Wolmer 2003, López-Hoffman et al. 2010).

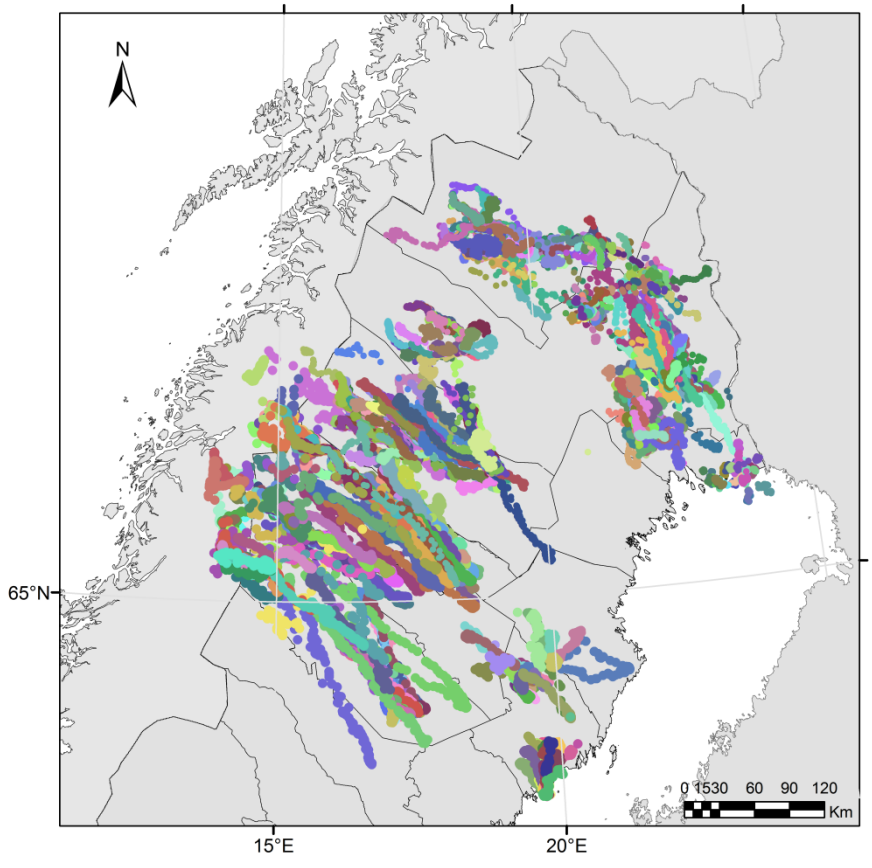


Figure 14 *- Migratory movements of moose in relation to existing boundaries of moose management areas (MMAs) in northern Sweden. Some improvements can be made to the directionality of the boundaries. It is also clear that transboundary collaborations are needed between Norway and Sweden since they share the same moose populations.*

Management is further compounded by how moose densities change through the year, since the scale of management would need to vary in space and time. Moose in the north migrate to mountainous habitats in spring and return to the lower-lying coniferous forests during winter. Moose also complete shorter spring migrations from coastal areas to more inland areas. This leads to more aggregated, high-density populations during winter compared to the more evenly distributed density of summer populations. Autumn migrations occur during November/December, whereas the principle management action of hunting occurs during September/October when moose are still in their

summer ranges. Meanwhile, forest damage usually occurs in the middle of winter, between January and March, when moose are on their winter range. Therefore, even though MMAs aim to encapsulate the annual range of moose, the scale of management of hunting is spatially and temporally disjointed from the management objective of reducing forest damage. Solving this challenge will require localised management actions at the scale of summer and winter ranges. An example of a management action would be to set adaptive hunting quotas. The adaptive hunting quota would be guided by knowledge of winter aggregation areas of moose and where these moose are distributed during the summer. Such an approach would clearly require an understanding of migratory pathways in order to predict the summer distributions, and is an example of a management approach that would vary in space and time in accordance to a species' movements. Alternatively, an adaptive hunting quota may reserve a portion of the quota that can only be fulfilled between January and March when moose have completed their migrations. However, a challenge in adopting such an approach will be to change hunter behaviour, for example changing hunter norms in terms of when harvest quotas are filled.

Another aspect of movement ecology that may complement the management of moose is to understand why moose aggregate in particular areas. These movement patterns may be influenced by factors like snow depth and available forage (Lavsund et al. 2003). The knowledge may be used to develop a vulnerability map of browsing damage (Tulloch et al. 2015). We found minimum productivity to be important for explaining variation in not only harvest rates but moose density as well, especially in areas with low harvest pressures (Paper VI). This knowledge may be useful for predicting densities of moose in the landscape and therefore possible aggregation areas, knowledge that may be important for developing alternative management actions. Management actions may include fencing vulnerable forest plantations, avoiding planting of economically important forest species in high threat areas, increasing hunting pressure or using measures that divert moose to a desired location. Research has shown that supplementary feeding (an artificial supply of food) may be a viable management tool for redistributing moose in the landscape after their migration, i.e. the winter range (Sahlsten et al. 2010, van Beest et al. 2010). However, browsing in areas near feeding stations may be intensified. Feeding stations could therefore be established in sacrifice areas and >1km from economically important forestry stands (van Beest et al. 2010). These actions are targeted at the winter distributions of moose when home ranges are smaller (~1,200 ha), thus refining the scale of management actions to more localised areas.

Finally, future changes and country wide policies may affect moose populations across the entirety of Sweden. Paper III illustrates how both the climate and landscape are important for influencing moose movements. Changes in policy, such as land-use change, may have direct knock on effects to the space use patterns of moose, with potential implications for species demography (Paper IV). The moose management system also needs to consider how future climate change may affect space-use patterns of moose (Paper III) and performance (Paper IV). Changes in precipitation patterns and vegetative productivity may lead to smaller scale movements in future (Paper III). However, the moose is a cold adapted species and temperature mediated changes need to be considered, such as how heat stress may affect performance (Lenarz et al. 2009) and space use patterns (van Beest and Milner 2013, Melin et al. 2014). Climate change has raised concerns about how disease and parasites may be influencing southerly populations already (Malmsten et al. 2014, Wünschmann et al. 2015). These challenges highlight how the scale of management needs to range from localised actions that target species seasonal ranges to landscape scales to incorporate species movements and finally a country-wide scale to incorporate changes occurring nationwide.

4.1.6 Step 4 – Implementation

The moose management system is well equipped for implementing management actions. Ongoing research of moose ecology, and continuing advances in technology and analytical approaches (Cagnacci et al. 2010, Tomkiewicz et al. 2010) enables an improved link between movement ecology and wildlife management and thus enables implementing knowledge-based actions. Furthermore, the moose management system adopts an adaptive style to management, which is needed when managing a complex and dynamic system like moose. Indeed, Williams (2011) describes the general features to which adaptive management are applied. This includes dynamic systems changing through time in response to environmental conditions, where the variation is only partially predictable, systems that are subject to management intervention and where effective management is limited by uncertainty. All of the features described by Williams (2011) are relevant to the management of mobile species like moose. Adaptive management also prepares wildlife managers for future uncertainties related to aspects such as land use and climate change, for instance, how changes in the predictability and stability of landscapes will influence the proportion of movement strategies in a population (Mueller et al. 2011), or how future changes will influence the timing of movements (McNamara et al. 2011).

The movement-management framework highlights implementation considerations like manpower, stakeholder interests, monitoring effort and human-wildlife conflict. It is fortunate that Sweden has such an active hunting population, where the hunters act as managers themselves, engage in monitoring efforts and contribute to research activities (Ericsson and Wallin 1999, Singh et al. 2014). Therefore, hunters and landowners implement management actions and act as citizen scientists. This increases the likelihood of achieving management objectives. Citizen science has been shown to be a successful form of stakeholder engagement (Dickinson et al. 2012). Citizen science also achieves scales of data collection and monitoring that would be difficult to achieve without their involvement (Bonney et al. 2009, Hurlbert and Liang 2012), and for example would be important for achieving the monitoring outcomes of Paper V. The inclusion of stakeholders in monitoring efforts, and in the decision making boards of the MMAs, increases the likelihood of them accepting proposed management actions and therefore increases the likelihood of achieving the management objectives (Redpath et al. 2013).

Finally, studies have also shown the importance of incorporating economic costs into the planning process (Naidoo et al. 2006). Implementing the strategies discussed in the above section (4.1.5) would involve costs that would need to be weighted. Management strategies that engage hunters will generally have low costs for the managing authority, and instead the costs are incurred by the hunter, such as hunting licenses, logistics and materials. Such a system works well when the incentive to hunt remains high, but some regions do not achieve the necessary levels of hunting required to control the population and have to resort to culling practices instead (Côté et al. 2004). Mismanaging hunting quotas may also have a large cost, such as an increase in wildlife-vehicle collisions or economic losses through browsing damage. Alternative management actions may also be considered in addition to hunting. Fencing vulnerable plantations may incur the greatest economic cost but may also include the highest potential gain due to the near-certain protection from browsing damage. However, fencing may restrict movements in the landscape and reduce connectivity, not only for moose but other species as well. Alternatively, supplementary feeding may incur a much lower cost but the benefit would be lower, since feeding stations would be placed in sacrifice areas where significant browsing damage may occur. Existing methods for decision theory enables managers to prioritise management actions with the greatest viability (Polasky et al. 2011). By understanding the movements of

moose, a larger number of viable management actions can be assessed for their implementation potential.

4.1.7 Step 5 – Evaluation

The importance of evaluating management strategies has grown recently, especially as studies highlight the uncertain outcomes of previously implemented management actions (Ferraro and Pattanayak 2006, Walsh et al. 2012). Evaluating management strategies is vital for determining how successful management actions are, and to guide future decision making. Therefore, management strategy evaluation is an integral component of adaptive management (Bunnefeld et al. 2011b). For managing moose, we have outlined three quantifiable management objectives that can be evaluated to determine the success of implemented management actions, i) setting harvest quotas that sustain a stable population, ii) keeping browsing damage to commercial forestry below a specified level and iii) a maximum level of wildlife-vehicle collisions per year. Evaluating whether management actions have achieved these objectives would be impossible without monitoring (Stem et al. 2005).

A number of monitoring actions are undertaken to estimate population sizes, and thus evaluate whether populations are stable. The principle methods for estimating population size of moose in Sweden are the hunter observation system, pellet counts, harvest statistics and aerial surveys (Rönnegård et al. 2008, Månsson et al. 2011, Singh and Ericsson 2014). The most widely used methods are the hunter observation system and pellet counts. However, the hunter observation system requires monitoring to be conducted at large scales (Sylvén 2000) and estimates are less accurate by giving an index of population size. The simplified cohort analysis described in Paper V provides an additional tool for accurately estimating population size. We have shown how it performs well and provides managers the opportunity to estimate populations at a variety of scales. The simplified cohort analysis contributes towards existing monitoring schemes and evaluation of management actions. Pending the reviews of Paper V, we hope to develop a web-tool that managers can use for estimating population size. Monitoring activities are also undertaken to evaluate the second and third objectives. Regular surveys are performed by forestry agencies to evaluate browsing damage that reduces timber-quality of commercially important species, such as browsing of top shoots, stem breakage and bark stripping (Månsson 2007). In addition, a national monitoring scheme is in place whereby drivers are required to report any vehicle collisions with moose and other deer species, which is managed by www.viltolycka.se.

This dissertation discusses a number of challenges and possible management actions that can be implemented. It is important that all three objectives described above are evaluated when implementing management actions. As an example, management actions targeted at reducing browsing damage may be prioritised in areas containing high winter densities of moose as predicted by vegetative productivity (Paper VI). The time that moose arrive in these areas is known (Paper II and III) and the scale of management can be guided by space use patterns during this time (Paper III). Furthermore, hunting quotas may be guided by knowledge of how the environment can influence performance (Paper IV) and by estimates of population size (Paper V). Evaluating the effectiveness of management actions would not only indicate whether the management objectives were achieved, but it would also inform future decision making. Adaptive management relies on knowledge-based actions, which should be an iterative cycle whereby new knowledge guides future decisions. For example, management strategy evaluation may provide new knowledge that improves our ability to determine harvest rates given our knowledge of vegetative productivity and moose density (Paper VI), and thus improve the spatial prioritisation of actions in the future.

4.2 Concluding Remarks

My thesis aims to strengthen the link between movement ecology and the management of mobile species. Understanding a species' movements improves our ability to identify the temporal and spatial scale of management. I use the moose as a case study of a species with complex movements whereby knowledge of movement ecology can directly inform wildlife management. I have attempted to keep my vision broad whilst keeping focus on the study species and the question at hand. I have been fortunate to cover a broad range of topics in my thesis whilst simultaneously maintaining a link between each chapter and the framework outlined in Paper I. My research on moose has been challenging yet inspiring at the same time. I have learnt a number of new methodologies and even provided guidance to newly emerging methods. I have also learnt to handle a variety of data sources and a constant challenge has been to match the temporal and spatial scales of different data sources. For example, I collected country-wide harvest data and I would encourage more standardised procedures for aggregating harvest data. The counties (läns) organise data at different scales, which may be at either district (kommun) or parish (församling) levels. These differences make it impossible to analyse the harvest data at a finer scale than the MMA, which is unfortunate and was a limiting factor in Papers V and VI. Nevertheless, we truly live in a data-rich age, and provided that data sources are managed appropriately, they provide exciting avenues for future research and new opportunities for wildlife management and conservation.

I addressed two important topics in my movement-focused papers. How to scale up movements to the population-level and how movement influences performance. I hope that the outcomes of my research will guide moose management by improving predictions of space use patterns and understanding how moose may respond to future change. There are several topics in moose movement ecology that I would like to investigate further. An example is improving our understanding of the decisions of female's regarding migration and parturition, and how this may interact with environmental conditions. I would also like to further explore the drivers of migration, especially since these drivers appear to vary across Sweden. Understanding these drivers will also guide future predictions of densities in the landscape and how these shift in space and time, which I touch on briefly in Paper V and VI. Despite other's concerns about the conservation value of investing in animal tracking studies, I feel that movement ecology will continue to grow given human's fascination of animal movements. My hope is that my thesis will ensure that current and future discoveries also contribute to species management and conservation.

5 Sammanfattning på svenska

Ett centralt mål inom naturresursförvaltning av den biologiska mångfalden är att identifiera det geografiska området. Traditionella metoder som områdesskydd syftar till att beskriva gränser, inom vilka arter kan förvaltas. Gränserna sätts bland annat utifrån mål för att gynna artmångfald eller utifrån politiska gränser, men misslyckas ofta med att ta hänsyn till hur arter för sig eller flyttar. En konsekvens är de utmaningar som kan uppstå när en individ lämnar ett avgränsat området som en nationalpark eller skogsparti. Det kan resultera i att djur skjuts olovligt - tjuvjakt - eller att djur kommer in i områden med mänsklig aktivitet och infrastruktur. En aktuell utmaning är att många arter inte kan förvaltas inom enbart ett område eftersom de flyttar över stora ytor; ett klassiskt exempel är flyttfåglar som häckar i ett land och övervintrar i ett annat. Dessa globala utmaningar understryker behovet av ökad kunskap om arters rörelser utanför tänkta förvaltningsområden, och behovet av att identifiera alternativa åtgärder som ökar flexibiliteten inom förvaltningen.

Min avhandling visar på ett tydligt sätt hur rörelseekologi kan användas inom förvaltning av vilda djur. Först beskriver jag hur ett konceptuellt ramverk som ger vägledning för hur rörelseekologi kan länkas till bevarande och viltförvaltning. Jag tillämpar ramverket i praktiken i fem studier som bygger på varandra sekventiellt genom att a) beskriva en metod som klassificerar och kvantifierar rörelser, b) förbättra vår förståelse om hur enskilda rörelser kan skalas upp till populationsmönster, c) länka individens rörlighet för till deras reproduktionsförmåga, d) skatta populationsstorleken från åldersspecifikt jaktdata och e) utvärdera jakt på älg i Sverige genom att applicera hypotesen ekosystemsutnyttjande). Modellarten för studierna i avhandlingen är älg (*Alces alces*) i Sverige, en art med varierande rörelsemönster i sitt utbredningsområde. Den förvaltas som normalt i avgränsade älgförvaltningsområden (t ex Sverige) eller viltförvaltningsenheter (t ex Kanada). Avhandlingen visar hur

rörelseekologi globalt kan användas i praktisk förvalting av mobila arter. Nationellt kompletterar den älgförvaltningssystemet i Sverige. Slutligen vill jag uppmuntra naturvårdare och viltförvaltare att utforska nya sätt att stärka kopplingen mellan rörelseekologi och förvaltning av mobila arter.

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Firstly I would like to thank my main supervisor Navinder Singh. There are a number of things to be thankful for, for giving me the opportunity to come to Sweden and be involved in this project, for all the guidance over the last four years and helping me develop as a researcher. I have enjoyed our many discussions about science in general and building ideas which I look forward to pursuing further in the future. I would also like to thank my co-supervisor Göran Ericsson for your guidance over the years, as well as sharing your knowledge about moose and your inputs into the chapters of my thesis.

I would also like to thank my collaborators and co-authors for being a part of my project and the numerous improvements they made to the chapters. I would especially like to thank Volker Radeloff and the rest of the SILVIS lab for hosting me during my research visit to UW-Madison and during the subsequent visits as well. I felt truly welcome and I learnt a lot during my time there. I have fond memories of the ski trip and sleeping on a sandbank during the canoe trip as a thunderstorm raged overhead whilst flood warnings were sent to our phones! Volker, I also appreciate the discussions we had and the advice you gave. I look forward to our ongoing and future collaboration.

Thank you to all the staff at VFM for making the last four years so enjoyable, and also to the senior researchers that provided their input along the way, especially those in the moose research group. I would also like to especially thank the field technicians that tirelessly collared the vast number of moose that make this project so unique.

To the PhDs of VFM (past and present), you have made this journey so much easier. I have enjoyed all the coffees, lunches, Rött's and general frölicks in the Swedish countryside (frolick is to move or play in a cheerful way ☺, and don't

forget the fröls either). It is not only the good times that will be remembered but also the support along the way. It is great having such a tight-knit group of PhDs to seek advice, discuss problems and overcome the hurdles of trying to finish. I wish you all the best as you finish your own PhDs, and if you are ever in the Netherlands be sure to drop by and say hi.

Special thanks go to all my family. When I decided to leave accountancy, I never quite envisaged becoming an academic and doing a PhD. Your support has been unwavering though and it is a strength to know that you are behind the decisions I make.

I then save the best for last, like the dessert after a meal, I thank the one dearest to my heart Anouschka. You have been there for me every step of the way, reassuring me when I was in doubt and picking me up when times were down. Thank you for your patience as I talk about my research and all the advice you have given along the way. I can honestly say that you are the best thing to have come out of my PhD ☺

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